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AVAILABILITY OF IRON AND MANGANESE IN SOUTHERN WISCONSIN LAKES FOR THE GROWTH OF *MICROCYSTIS AERUGINOSA*¹

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The occurrence of essential elements in lakes and streams in both soluble and insoluble forms makes it difficult to evaluate their availability for phytoplankton growth by chemical analysis of water samples. This is particularly true for iron and manganese, elements which form compounds of very slight solubility at alkaline pH values and which tend to form less soluble compounds as they change in valence with the marked shift in oxidation-reduction conditions between the bottom layers and the surface of a lake. It seemed reasonable, therefore, to believe that changes in the availability of iron and manganese might be a governing factor in the nutrition and perhaps in the succession or cyclic occurrence of nuisance blooms of blue-green algae.

The role of iron in phytoplankton production has indeed been considered by various investigators in the past. Gran (1933) suggested that the soluble iron compounds washed out with humus from the shore might explain the relatively great phytoplankton productivity of coastal waters in comparison with the open ocean. Harvey (1938) believed the soluble iron present in sea water was far too low to provide the quantities required by diatoms and suggested that colloidal and larger particles of ferric hydroxide or phosphate might be utilized by these organisms. Rodhe (1948) evaluated the supply of available iron in lake water by comparing algal growth in samples enriched with nitrogen and phosphorus and in synthetic culture solutions containing various levels of iron.

He concluded that in general nitrogen and phosphorus were more likely to become limiting for algal growth under natural conditions than was iron, although in lakes heavily fertilized with nitrogen and phosphorus through pollution iron availability might become important. Lund (1950) considered present knowledge insufficient for any decisions on how algae obtain iron, how much is in the cells, or what is the minimal quantity necessary for their growth.

The availability of manganese for growth of algae apparently has received only limited attention. Harvey (1949) considered it improbable that the manganese content of lake and river water would limit their productivity. On the other extreme, Guseva (1939) suggested that the high manganese content associated with the beginning of the overturn the second year after flooding of the Uchinskii reservoir was actually toxic to phytoplankton.

Fogg (1955) recently has presented evidence that extracellular polypeptides secreted by algae are able to form soluble chemical complexes with metals and suggests this may be of importance in maintaining certain essential elements in available forms. This could apply to both iron and manganese.

The present paper presents results of an evaluation of the availability of iron and manganese for the growth of *Microcystis aeruginosa* in southern Wisconsin lakes and a study of several factors which affect the availability of those elements.

EXPERIMENTAL PROCEDURE

The bloom-producing blue-green alga *Microcystis aeruginosa* was employed in all experiments to be reported. The general culture medium and culture conditions were as described previously (Gerloff, Fitzgerald, and Skoog 1952). A variation in iron and manganese sources was necessary,

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however, to prevent formation in the culture medium of precipitates of these elements which would be collected with the algae during centrifugation and prevent accurate analysis of cellular iron and manganese. This was accomplished by substituting iron and manganese chelates with EDTA (Ethylene Diamine Tetra Acetic Acid) for the ferric citrate and manganese chloride salts previously employed.

IRON AND MANGANESE CONTENTS OF MICROCYSTIS

A procedure similar to that employed for evaluating nitrogen and phosphorus supplies in lakes, *i.e.* by comparisons of the contents of the elements in algae collected from lake blooms with the critical contents (minimum levels for maximum growth) established in the laboratory, was employed to determine iron and manganese availability to *Microcystis*.

The yield and iron content of *Microcystis* cultured in solutions of varying iron concentration were first determined. It was found (Table I) that very small amounts of iron were adequate for maximum growth, for only when the element was omitted (Treatment A) was there a significant decrease in growth. The critical level of iron in the cells may be considered as approximately 100 ppm, the content in Treatments A, B, and C. In Treatments D to H the cellular iron

TABLE I. Dry weight and iron content of *Microcystis* cultured for 14 days in solutions containing varying levels of chelated Fe

Treatment	Fe added, ppm	Dry wt. of algae, mg/l	Fe content of cells, ppm
A.....	0.000	185	99
B.....	0.005	250	95
C.....	0.010	259	103
D.....	0.015	268	123
E.....	0.020	265	138
F.....	0.040	270	160
G.....	0.060	272	180
H.....	0.100	264	222

content continued to increase without an effect on yield to a maximum of 222 ppm. In similar experiments with iron concentrations greater than the 0.1 ppm in Treatment H, cell contents in excess of 400 ppm have been obtained.

The iron contents of twelve samples of *Microcystis* collected from lake blooms are presented in Table II. All samples, with the exception of two (from Nagawicka in 1953 and Waubesa in 1954) have values in excess of 200 ppm, the highest being 543 ppm. From comparisons with the 100 ppm critical level, there seems no reason

TABLE II. The iron and manganese contents of *Microcystis* collected from blooms in southern Wisconsin during 1953 and 1954

Lake sampled	Date sampled	Fe content of algae, ppm	Mn content of algae, ppm
Waubesa.....	8/ 8/53	246	92
Spaulding Pond..	8/ 9/53	360	232
Delavan.....	8/18/53	345	42
Pewaukee.....	8/21/53	458	57
North.....	8/21/53	543	53
Nagawicka.....	8/21/53	164	13
Monona.....	8/25/53	396	80
Monona.....	8/30/53	272	46
Monona.....	9/ 1/53	330	47
Monona.....	9/ 3/53	298	35
Waubesa.....	8/17/54	185	36
Nagawicka.....	8/19/54	509	89

to believe, therefore, that iron availability limited the growth of *Microcystis* in the lakes sampled.

The results of Table III show that the critical cell content of manganese is extremely low, for maximum growth was obtained even when the element was not added to the culture medium (Treatment A) and the cell content was only 4 ppm. In additional experiments, not reported because the yields of cells were insufficient for manganese analyses, decreases in growth were obtained when manganese was omitted from the culture medium and the degree of growth response from very small additions indicated the critical level to be less than 10 ppm.

TABLE III. Dry weight and manganese content of *Microcystis* cultured in nutrient solutions containing various levels of chelated manganese

Treatment	Mn added, ppm	Dry wt. of algae, mg/l	Mn content of cells, ppm
A.....	0.000	199	4
B.....	0.002	202	10
C.....	0.010	200	16
D.....	0.020	212	13

Examination of the manganese contents of algae from lake blooms, also reported in Table II, gives no indication that this element had limited growth, because all values are more than twice and most of them many times greater than the critical level of approximately 4 ppm. The conclusion that manganese is present in ample supply for growth is substantiated by the laboratory findings that only nitrogen, phosphorus, and iron need be added to lake water cultures to obtain growth comparable to that in optimal synthetic media.

EFFECT OF VARYING IRON-MANGANESE RATIOS

Detailed chemical analyses of a large number of

water samples systematically taken from various depths in Lake Mendota at different times of the year have been carried out by Prof. G. A. Rohlich and associates in the Sanitary Eng. Dept., University of Wisconsin. With their permission, some of the analyses for iron and manganese are presented in Table IV. The data show that in every sample the total content of manganese exceeded that of iron. In view of this, the critical iron content of algae collected from lakes might be higher than the value established for laboratory-cultured organisms grown in solutions in which the iron concentration usually exceeded that of manganese. Experience with higher plants (Somers and Shive 1942) has shown that the optimum iron concentration varies with the supply of manganese. A level of iron that is adequate at relatively low concentrations of manganese may result in chlorosis brought on by iron deficiency at higher manganese concentrations.

TABLE IV. Total iron and manganese contents of water samples taken from various depths of Lake Mendota and at different times of the year

Date sampled	ELEMENT CONTENT IN PPM AT					
	Surface		10 meter depth		0.5 meter above bottom	
	Fe	Mn	Fe	Mn	Fe	Mn
7/21/48.	0.015	0.093	0.011	0.133	0.046	0.650
8/ 5/48.	0.002	0.160	0.000	0.147	0.056	0.673
8/23/48.	0.002	0.035	0.004	0.053	0.079	0.484
9/27/48.	0.003	0.117	0.005	0.110	0.083	0.507
10/18/48.	0.015	0.120	0.023	0.140	0.019	0.123
11/ 8/48.	0.003	0.120	0.008	0.117	0.075	0.390
11/30/48.	0.003	0.134	0.006	0.104	0.003	0.119
1/ 4/49.	0.007	0.113	0.000	0.100	0.005	0.093
2/ 9/49.	0.022	0.150	0.021	0.093	0.023	0.463
3/ 1/49.	0.017	0.117	0.004	0.103	0.075	0.433
4/ 4/49.	0.031	0.114	0.045	0.117	0.039	0.153
5/ 3/49.	0.033	0.073	0.028	0.070	0.018	0.093

Each value reported is an average of samples from three stations at which the depth varied from 65 to 80 feet. The data in this table are from Prof. G. A. Rohlich and associates, Sanitary Eng. Dept., Univ. of Wis.

The results in Table V show similar iron-manganese relationships in the case of algae. For example, in cultures with a constant 0.02 ppm iron supply and with increasing concentrations of manganese (Treatments F to J), optimum yield was with 0.02 ppm manganese (Treatment G) and there was a sharp decrease in growth with each successive increase in manganese supply until in Treatment J with 1.00 ppm manganese the yield was less than ten per cent of the optimum. The alleviation of the "high manganese toxicity" by additional iron is clearly shown by the increase in yield from 3 to 177 mg. through the series of Treatments E, J, O, and T with the manganese

TABLE V. The effect of the manganese concentration in the culture solution on the iron requirement of *Microcystis*

Treatment	CONC. IN CULTURE SOLN., PPM		Dry wt. of algae, mg/1
	Fe	Mn	
A.....	0.00	0.00	142
B.....	"	0.02	173
C.....	"	0.10	142
D.....	"	0.50	18
E.....	"	1.00	3
F.....	0.02	0.00	250
G.....	"	0.02	251
H.....	"	0.10	189
I.....	"	0.50	98
J.....	"	1.00	21
K.....	0.05	0.00	272
L.....	"	0.02	268
M.....	"	0.10	290
N.....	"	0.50	177
O.....	"	1.00	63
P.....	0.10	0.00	286
Q.....	"	0.02	283
R.....	"	0.10	271
S.....	"	0.50	255
T.....	"	1.00	177

content at 1.00 ppm and increasing iron levels of 0.00, 0.02, 0.05, and 0.10 ppm respectively.

Even though the iron requirement for *Microcystis* varies with the manganese concentration and the manganese content of lake water is relatively high (Table IV), the total iron and manganese contents of algae from lake blooms reported in Table II make it seem doubtful that the manganese concentrations in the lake water were high enough to have made the availability of iron a limiting factor for growth, because all algal samples contained much greater amounts of iron than of manganese. In fact, except in the samples from Spaulding Pond and Waubesa with iron: manganese ratios of 3:2 and 5:2 respectively, the ratios were in the range from 5:1 to 13:1.

EXCESS MANGANESE AND VARYING CALCIUM-MANGANESE RATIOS

Laboratory experiments had shown that as little as 0.2 ppm manganese in the synthetic culture solution decreased the yield of *Microcystis*. Although the surface layers of stratified lakes are generally low in manganese, the concentrations near the bottom frequently exceed 0.2 ppm. It was thought, therefore, that often the lower strata and sometimes most of the lake volume (*i.e.*, under conditions of rapid mixing of the water by wind and current action) might have such a high

manganese content that growth of algae would be suppressed.

To determine if the high manganese content of bottom water actually is toxic to algae, samples of water collected from the surface and from within 0.5 meter of the bottom of Lake Mendota were enriched with nitrogen, phosphorus, and iron, and were then autoclaved and inoculated with *Microcystis*. Analyses failed to detect manganese in the surface water, but in the bottom layer 0.87 ppm was found in one case and 1.85 ppm in another. Surprisingly, the algae grew excellently in all samples. It was further shown in a laboratory experiment (Table VI) that manganese was much less toxic when added to lake water than expected on the basis of results with nutrient solutions. Even 4.0 ppm manganese had no effect on *Microcystis* growth in lake water whereas 0.2 ppm gave a decrease in yield in the synthetic solution.

TABLE VI. Comparison of the toxic effects of various levels of manganese to *Microcystis* cultured in a synthetic medium and in enriched lake water

Treatment	Culture medium	Mn. added, ppm	Dry wt. of algae, mg/l	Algae count, cells/mm ³	Relative growth
A.....	Synthetic	0.02	192		100
B.....		0.10	183		95
C.....		0.20	168		88
D.....		0.50	103		54
E.....		1.00	63		33
F.....		2.00	18		9
G.....	Enriched lake water*	0.05	...	11,000	100
H.....		0.10	...	11,450	105
I.....		0.20	...	11,000	100
J.....		0.50	...	11,750	107
K.....		1.00	...	12,700	115
L.....		2.00	...	11,700	106
M.....		4.00	...	10,850	99

*Lake water with 20.4 ppm N as NaNO_3 , 1.8 ppm P as Na_2HPO_4 , and 0.56 ppm Fe as ferric citrate added.

A principal difference between the two types of cultures was that the synthetic solution contained only 0.5 ppm calcium which is far below the concentration in the hard Lake Mendota water. The results presented in Table VII show that this difference in calcium content very likely accounts for the difference in the toxicity of manganese in the two media. With 0.5 ppm calcium in the culture solution, 0.5 ppm manganese was slightly toxic and 2.00 ppm stopped growth completely. However, with 10.00 ppm calcium present, 0.50 ppm manganese did not significantly inhibit growth and even 4.0 ppm only slightly reduced the yield. It seems obvious from these results that the existing antagonism between manganese and calcium in hard water lakes makes it unlikely that even

TABLE VII. Effect of calcium content of the culture medium on the toxicity of manganese to *Microcystis*

Treatment	ELEMENT ADDED, PPM		Dry wt. of algae, mg/l	Relative growth
	Ca	Mn		
A.....	0.5	0.05	302	100
B.....	"	0.10	280	93
C.....	"	0.20	280	93
D.....	"	0.50	247	82
E.....	"	1.00	129	43
F.....	"	2.00	No growth	...
G.....	"	4.00	No growth	...
H.....	10.0	0.05	163	100
I.....	"	0.10	173	106
J.....	"	0.20	159	98
K.....	"	0.50	153	94
L.....	"	1.00	145	89
M.....	"	2.00	120	74
N.....	"	4.00	112	69

the very high levels of manganese sometimes present would interfere with *Microcystis* growth and bloom development.

The possibility that a similar antagonism between calcium and iron would raise the iron requirement of lake algae above the critical value determined in the laboratory was also investigated. The first experiments indicated that this might be true, as more iron was required to produce maximum growth with 10.0 ppm calcium in the medium than with 0.5 ppm. However, during autoclaving of the solutions with the higher calcium content, a calcium phosphate precipitate was formed, and the iron might, therefore, become less available to the algae through coprecipitation with or adsorption onto this precipitate.

Attempts to avoid precipitation through chelation of calcium, iron, and the essential trace elements with EDTA were completely unsatisfactory. Whereas it was possible to develop a basal medium in which these elements were chelated and which would provide for excellent growth of *Microcystis*, it was impossible to markedly increase or decrease the level of one chelated element without correspondingly changing the others.

Separate autoclaving of iron and phosphorus sources eventually proved an effective means of avoiding precipitate formation. With the adoption of this precaution, the level of calcium in the culture medium had absolutely no effect on the iron requirement of the algae. It is not likely, therefore, that the relatively high calcium concentrations in lakes would affect the requirement of the algae for soluble iron.

REQUIREMENTS AT VARYING LIGHT INTENSITIES

It had been noted that light intensities in excess of the 100 ft-candles routinely employed for culturing *Microcystis* produced chlorotic cells and

decreased yields. Because of their role in chlorophyll formation, it seemed possible that increased iron or manganese levels might offset these adverse effects, and also that differences in light intensity might bring about different requirements for iron and manganese by the algae when cultured in the laboratory and when growing in the lakes. However, at a high light intensity (500 ft-candles) the algae grew poorly and were yellow in color regardless of variations in concentration of iron or manganese or both elements in the culture solution.

DISCUSSION

The demonstrated antagonisms between iron and manganese and between calcium and manganese together with known variations in iron and manganese solubilities associated with changes in pH and oxidation-reduction potentials make it clear that the optimal levels of these elements must vary over a considerable range and may change abruptly with conditions within a lake or from one lake to another. The present comparisons of the iron and manganese contents of *Microcystis* from lake blooms with the critical levels of these elements established in the laboratory, therefore, represent approximations. Nevertheless for practical purposes, they permit a rather accurate evaluation of the availability of these elements in lakes in relation to requirements for growth.

There are, of course, numerous sources of error in this procedure. For example, iron and manganese may tend to be precipitated and adhere to the surfaces of the algal colonies, thus making the iron and manganese contents appear to be higher than they actually are inside the living cells. Harvey (1938) found that colloidal iron was adsorbed onto marine diatoms and that the organisms were able to utilize the element from this source. The exact extent to which inert deposits may have been included in the present determinations is difficult to estimate, but since the differences between required levels and those actually found are very large, it is doubtful that this source of error would significantly affect the conclusions reached above.

Although the demonstrated antagonism between calcium and manganese would seem to eliminate manganese toxicity as a factor in bloom development, it might be argued that the high calcium content in the lake water could raise the critical level of manganese to a higher value than that established in the laboratory and thus effectively lead to manganese deficiency. This seems doubtful in view of the fact that it has never been neces-

sary to add manganese but only nitrogen, phosphorus, and iron to laboratory cultures of autoclaved water from a number of lakes in order to obtain growth far in excess of the amounts of algae produced per volume of water in the severest lake blooms.

Considering the various aspects of the problem, therefore, it is concluded from the data obtained that neither iron nor manganese supply is limiting the development of blooms of *Microcystis* in the lakes sampled.

SUMMARY

The availability of iron and manganese for the growth and development of blooms of *Microcystis aeruginosa* in southern Wisconsin lakes has been investigated. Comparisons were made of the cell contents of these elements in algae collected from blooms with the critical levels of the elements for maximum growth determined in the laboratory. These critical levels were approximately 100 ppm iron and 4 ppm manganese. The cell contents of the elements were in all cases so far in excess of these values that it seems unlikely the availability of either element is a factor in the development of blooms of this species in lakes.

Antagonistic relationships between manganese and iron and between calcium and manganese were demonstrated. These contribute to the difficulty of determining exact levels of iron and manganese required in nutrient media, but are judged not to be serious enough to significantly affect the accuracy of the determinations of the critical levels or the conclusions drawn as to the availability of the elements for growth of *Microcystis*.

The manganese content of lake waters appears to reach levels high enough to be toxic to the algae were it not for an antagonistic action of calcium which is also present in relatively high concentrations.

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NITROGEN AS A LIMITING FACTOR FOR THE GROWTH OF *MICROCYSTIS AERUGINOSA* IN SOUTHERN WISCONSIN LAKES¹

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Nitrogen and phosphorus generally have been considered the nutrient elements most likely to limit growth of phytoplankton in lakes and streams (Hutchinson 1944; Rodhe 1948). However, a review of the literature shows that agreement has not been reached and that the observational data are inadequate for a decision as to which element may be available in least abundant supply relative to actual requirements for growth of the algae (Riley 1940; Sawyer 1943, 1945; Deevey 1940). The shortcomings have been discussed earlier (Gerloff and Skoog 1954) of conclusions based merely on comparisons of chemical composition of waters in the presence or absence of blooms or based solely on determinations of nutrient concentration requirements in batch cultures in the laboratory and comparisons of these levels with those found in natural waters.

A procedure was reported (Gerloff and Skoog 1954) in which the actual cell content of an essential element in cells of *Microcystis aeruginosa* as compared with its "critical level" is used as an index of its availability to the algae. The critical levels of nitrogen, phosphorus, iron, and manganese, that is, the minimum cell content of each of these elements required for maximum growth, were established in laboratory experiments and compared with the levels found in samples of this alga collected from lake blooms (Gerloff and Skoog 1954, 1956). Nitrogen was found in relatively less abundant supply than any other essential element, but there was no proof that the levels were sufficiently low to be limiting the growth of the alga in the lakes sampled.

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The present paper presents a refinement in the procedure which when applied to the reported data does indicate that the availability of nitrogen is actually limiting growth. This has led to several more general considerations of nitrogen and phosphorus nutrition in lakes, certain aspects of which also are considered here.

The experimental procedures employed were presented in previous papers (Gerloff *et al.* 1952; Gerloff and Skoog 1954), and only necessary deviations from these will be described. *Microcystis aeruginosa* was employed in all experiments, because it is one of the most common bloom-producing organisms in this area and is convenient to handle in laboratory experiments.

GROWTH OF *MICROCYSTIS* IN ENRICHED LAKE WATER

By determining the growth (weights or cell counts) of algae in definite volumes of lake water after enrichment with various combinations of essential mineral elements, the order of availability of the elements relative to need can be estimated with fair accuracy. Data from an experiment of this type are presented in Table I. *Microcystis* was cultured in surface water from two lakes at Madison, Wisconsin, after enrichment with nitrogen, phosphorus, iron and other essential elements at concentrations present in the synthetic medium routinely employed in laboratory experiments. Growth is expressed as cell numbers determined with a haemocytometer counting chamber, because the presence of precipitates and suspended matter made it impractical to use weight measurements.

Unenriched lake water (Treatment A) may be seen to support very poor growth. On the other hand, the addition of only nitrogen, phosphorus, and iron to the lake water (Treatment H) resulted in as great yields as were obtained with all elements added (Treatment I) and nearly as great as with the complete synthetic nutrient solution (Treatment J).

TABLE I. Growth of *Microcystis aeruginosa* in surface water from Lakes Mendota and Waubesa with and without additions of essential mineral elements. Culture period from May 3 to May 17, 1950

Treatment	Autoclaved water plus	MENDOTA WATER		WAUBESA WATER	
		Algae count, cells/mm ³	Rel. growth, % of Treat. H	Algae count, cells/mm ³	Rel. growth, % of Treat. H
A.....	No additions	560	6	1,523	14
B.....	NO ₃	5,780	64	7,737	73
C.....	PO ₄	500	6	1,101	10
D.....	Fe	495	6	1,139	11
E.....	PO ₄ and Fe	400	4	874	8
F.....	NO ₃ and Fe	4,310	48	9,675	92
G.....	PO ₄ and NO ₃	6,300	70	7,575	72
H.....	NO ₃ , PO ₄ , and Fe	9,030	100	10,575	100
I.....	All essential elements	7,590	84	9,875	93
J.....	Synthetic Nut. Soln.	10,235	113	10,235	97

The number of cells added as inoculum (approximately 100 per mm³) has not been subtracted from the cell counts.

A comparison of cell counts in Treatments B, C, and D in the which nitrogen, phosphorus, or iron was added to the lake water singly and particularly in Treatments E, F, and G in which these three elements were added in combinations of two elements clearly shows that nitrogen was the primary limiting factor for *Microcystis* growth. For example, in Lake Mendota water the addition of only phosphate or iron produced no increase in growth while the addition of nitrate alone resulted in approximately 64 per cent of the growth obtained with all three elements added (Treatments A to D). Nitrogen, phosphorus, and iron were limiting factors for growth in Treatments E, F, and G respectively, and the data show that the Mendota water contained enough nitrogen for only four per cent of maximum growth as compared with enough phosphorus for 48 per cent and iron for 70 per cent of the maximum growth. The requirement for added iron in the lake water is not due to possible precipitation of this element by the autoclaving, because iron was similarly required when the lake water was sterilized by filtration.

The results with Lake Waubesa water are very similar to those with the Mendota water. However, part of the sewage effluent from the Madison disposal plant is discharged into Lake Waubesa and its fertilizing effect is apparent from the greater growth in unenriched water (Treatment A). From a comparison of growth in water from the two lakes enriched with only nitrogen and iron (Treatment F), it also is apparent that the effluent is particularly rich in phosphorus. Lake Mendota water contained sufficient phosphorus for only

48 per cent of maximum growth, but Lake Waubesa water provided phosphorus for 92 per cent of the maximum.

Conclusions from experiments of this type are limited in their application as the samples of water represent conditions only in very limited areas of the lake and at a specific time. Even if the tests were expanded to include samples from various depths, locations, and time of the year, they would still be inadequate to answer questions of nutrient availability, because factors such as the effective volumes of water from which elements are absorbed, rates of absorption, and rates of replacement of available forms are ignored.

Nevertheless, as far as they go, the results of these tests indicate that only nitrogen, phosphorus, and iron need be considered possible limiting elements and of these nitrogen is much more critical than either phosphorus or iron.

NITROGEN AND PHOSPHORUS REQUIREMENTS OF MICROCYSTIS

In the earlier report (Gerloff *et al.* 1952) nitrogen and phosphorus requirements were not determined with the precision needed in the present investigation. Algae therefore were cultured in solutions in which the elements were varied in smaller steps, nitrogen by increments of one ppm and phosphorus by a fraction of a ppm. The graphs of Figures 1 and 2 show a direct proportionality between yield and nitrogen or phosphorus content within the range of concentrations presented. At still higher concentrations, a constant maximum level is of course reached (Gerloff and Skoog 1954). Approximately 5 mg of nitrogen and 0.08 mg of phosphorus were necessary for each 100 mg of algae produced. This corresponds to a N:P ratio of 60:1, a value which was compared with the ratios of these elements which exist in lake water samples from various depths and locations throughout the year (Table II). These data were available from analyses carried out by Prof. G. A. Rohlich and associates, Dept. of Sanitary Eng., University of Wisconsin. Although various forms of nitrogen and phosphorus were determined, for simplification in presentation all forms have been combined as total nitrogen and total phosphorus.

It is readily apparent that while the N:P ratios vary with the time of year and the depth at which samples were taken, they never exceeded 10:1, which is far from the permissible limit of 60:1 established in the laboratory.

The ratios of soluble nitrogen to soluble phosphorus would perhaps be of greater interest than the ratios of total amounts in estimating the extent to which the elements are available to the algae.

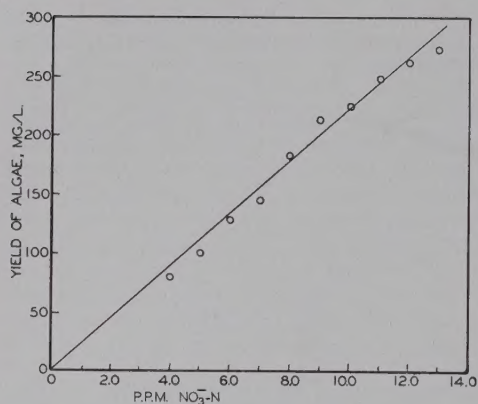


FIG. 1. Relationship between yield of *Microcystis aeruginosa* and the concentration of nitrogen added to the culture medium. The plotted data are average values from three separate experiments.

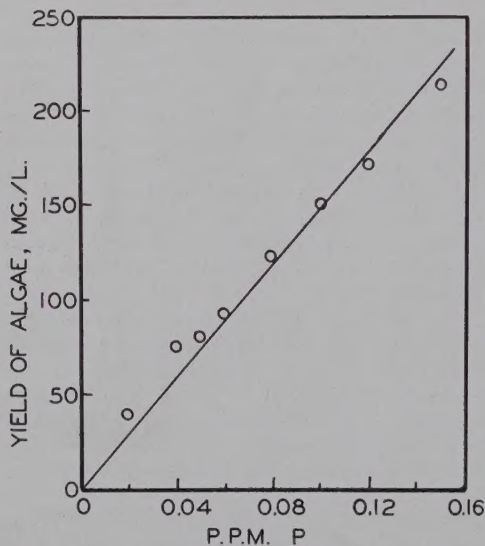


FIG. 2. Relationship between yield of *Microcystis aeruginosa* and the concentration of phosphorus added to the culture medium. The plotted data are average values from three separate experiments.

Determinations of soluble nitrogen and phosphorus are actually included in the data of Table II. However, the inaccuracy of analyses for the extremely small quantities of soluble nitrogen and soluble phosphorus present in lake water makes calculations from these data of doubtful value. For example, the soluble nitrogen content in the surface water on Aug. 5, 1948, was 0.031 ppm. One-sixtieth of this amount of phosphorus or ap-

TABLE II. Total nitrogen and phosphorus contents and ratios of water samples collected throughout the year from various depths of Lake Mendota

Date sampled	SURFACE			10 METER DEPTH			0.5 METER ABOVE BOTTOM		
	Tot. N	Tot. P	N:P	Tot. N	Tot. P	N:P	Tot. N	Tot. P	N:P
7/21/48.	0.304	0.061	6.0	0.455	0.071	6.4	0.851	0.463	1.8
8/ 5/48.	0.454	0.061	7.4	0.781	0.079	9.9	0.710	0.599	1.2
8/23/48.	0.594	0.133	4.5	0.709	0.109	6.5	1.166	0.467	2.5
9/27/48.	0.513	0.096	5.3	0.546	0.141	3.9	1.609	0.357	4.5
10/18/48.	0.553	0.183	3.0	0.481	0.196	2.5	0.477	0.215	2.2
11/ 8/48.	0.768	0.166	4.6	0.611	0.196	3.1	0.710	0.190	3.7
11/30/48.	0.566	0.254	2.2	0.533	0.251	2.1	0.468	0.238	2.0
1/ 4/49.	1.042	0.287	3.6	1.085	0.277	3.9	0.993	0.289	3.4
2/ 9/49.	0.814	0.156	5.2	0.833	0.147	5.7	1.075	0.169	6.4
3/ 1/49.	0.478	0.209	2.3	1.111	0.207	5.4	0.997	0.231	4.3
4/ 4/49.	0.869	0.237	3.7	0.891	0.287	3.1	0.789	0.233	3.4
5/ 3/49.	0.590	0.200	3.0	0.689	0.169	4.1	0.524	0.193	2.7

The data in this table are from Prof. G. A. Rohlich and associates, Sanitary Eng. Dept., University of Wisconsin. Each value represented is an average of samples from three stations at which the depth varied from 65 to 80 feet.

proximately 0.0005 ppm would satisfy the minimum requirements of the algae. The soluble phosphorus content actually reported was 0.001 ppm, which could seem to be adequate. It is doubtful, however, if it is possible to make valid distinctions between phosphorus concentrations in this low range even though the differences might be significant for algal growth. Lund (1950) also considers 0.001 ppm as the limit of accurate phosphorus determination. During winter months when the lake is unstratified and algal growth is not abundant, the soluble nitrogen and soluble phosphorus contents increase to values that can be determined with reasonable accuracy. The values for soluble N:soluble P, like those for total N:total P, are then much less than 60:1.

CELL CONTENT OF NITROGEN AND PHOSPHORUS

The minimum cell contents of nitrogen and phosphorus necessary for maximum growth of *Microcystis* (critical levels) initially were determined to be 4.5 per cent nitrogen and 0.20 per cent phosphorus in laboratory experiments. However, subsequent work (including the results presented in Figures 1 and 2) has shown that 4.0 per cent nitrogen and 0.12 per cent phosphorus are more nearly correct. All comparisons of the nitrogen and phosphorus contents of lake algae with these critical levels have indicated nitrogen to be in relatively less abundant supply than phosphorus, but even the nitrogen content was also always sufficiently above the critical level so that it need not necessarily have been the limiting factor for growth.

In this connection it was noted that the amount of the gelatinous sheath material was greater in laboratory cultures than in cell samples collected from the lakes. This, of course, would be ex-

pected because with the bacteria-free laboratory cultures most if not all the sheath material formed during the entire growth period would be harvested by centrifugation whereas with the lake samples the sheath might be sloughed off, worn away, or degraded by microorganisms prior to their collection. As the sheath material is mainly carbohydrate, this would result in relatively higher critical levels for the lake algae.

For lack of suitable procedures, analyses for specific sheath constituents were not attempted. Instead determinations were made by the anthrone test (Morris 1948) for carbohydrate content, including the sheath, of the algae samples from various sources. The results are reported as glucose equivalents of total carbohydrate per 100 micrograms of algae.

As shown in Table III, the increase in carbohydrate content with age of *Microcystis* cultures in the laboratory is indeed very great, from a glucose equivalent of 33 at six days to 68 at fourteen days after inoculation. During this period, the total dry weight increased from 68 to 195 mg per liter. As fourteen-day old cultures (approximately 200 mg/1 dry wt.) were used for determinations of the critical levels of nitrogen and phosphorus, their glucose equivalent was further checked in a total of five experiments. The average value obtained was 67, and this value will be employed in subsequent calculations.

TABLE III. Dry weight, total nitrogen content, and total carbohydrate content of *Microcystis* at successive intervals of a fourteen-day culture period. Average values of two separate experiments

Treatment	Days after inoculation	Dry wt. of algae, mg/l	Total N, per cent	Glucose equivalent*
A.....	6	58	9.1	33
B.....	8	105	9.0	39
C.....	10	140	8.4	47
D.....	12	175	7.7	55
E.....	14	195	6.5	68

*100 micrograms of algae contained carbohydrate equivalent to the indicated micrograms of glucose.

Anthrone analyses of *Microcystis* collected from blooms in a number of southern Wisconsin lakes are presented in Table IV. It is immediately apparent that the glucose equivalents are much below 67. They correspond rather to those of only six to eight day old cultures, and thus confirm the suspicion that the carbohydrate content was lower and therefore the critical nitrogen and phosphorus levels would be higher for the lake samples than for the fourteen-day-old laboratory cultures.

TABLE IV. Comparisons of the nitrogen and phosphorus contents of *Microcystis* collected from lake blooms with critical nitrogen and phosphorus levels* before and after correcting for variations in carbohydrate content

Lake sampled	Date sampled	Glucose equivalent*	N CONTENT, %		P CONTENT, %	
			Original	Corrected	Original	Corrected
Spaulding.....	8/ 9/53	32	7.61	5.02	0.62	0.41
Delavan.....	8/18/53	29	6.97	4.16	0.33	0.20
North.....	8/21/53	35	6.28	3.91	0.67	0.42
Nagawicka.....	8/21/53	46	5.43	3.88	0.22	0.16
Monona.....	8/30/53	35	6.76	4.40	0.44	0.26
Monona.....	9/ 1/53	40	6.15	4.15	0.41	0.28
Nagawicka.....	8/19/54	35	6.57	4.20		
Waubesa.....	8/17/54	39	7.10	4.90		
Waubesa.....	8/20/54	40	6.33	4.43		

*100 micrograms of algae contained carbohydrate equivalent to the indicated micrograms of glucose.

The obvious next step was to compare the nitrogen and phosphorus contents of field-collected algae with those of laboratory cultures having similar carbohydrate contents. This was made possible by further reference to Table III where it may be seen that the increase in glucose equivalent from 33 to 68 is associated with a drop in nitrogen content of the cells from 9.1 to 6.5 per cent. This corresponds to an average decrease of 0.74 per cent in the nitrogen content for each rise of 10 in the glucose equivalent. This value, therefore, has been used to adjust the nitrogen and phosphorus contents of the lake bloom algae to the contents that would be present if the glucose equivalent were equal to that of the fourteen-day laboratory cultures.

The corrected values were then compared with the 4.0 per cent nitrogen critical level in Table IV. When it is considered that the nitrogen content of *Microcystis* may reach as high as 9.0 per cent, it is striking how close the corrected values are in all cases to the critical percentage of 4.0. In fact, samples from two lakes (North and Nagawicka in 1953) are slightly below the 4.0 per cent value, and thus indicate that in these lakes nitrogen supply had become limiting for growth.

Several additional interesting correlations can be made between these corrected values and field observations. In the first place, the algae from Spaulding Pond and Lake Waubesa have the two highest nitrogen contents and these lakes are notorious for supporting almost continuous, heavy blooms. On the other hand, the two lowest values, from the North and Nagawicka lake samples of 1953, check with field records describing the yellowish-green appearance of these blooms. Furthermore, the serial samples from Lake Monona in 1953 and from Lake Waubesa in 1954 were taken

purposely at intervals of several days during the development of *Microcystis* blooms to determine if a decrease in cell content of nitrogen could be detected as growth of algae in the water increased. In both cases, the second sample contains considerably less nitrogen than the first, and in the Monona samples the content was reduced almost to the critical level.

The phosphorus contents of the lake algae were also "corrected" by reducing them in the same proportions as the nitrogen values. As shown in Table IV, the corrected levels in all cases are considerably in excess of the 0.12 per cent critical percentage. In fact, in four of the six samples for which phosphorus analyses are available, the phosphorus content of lake algae was more than twice the level estimated to be limiting for growth.

DISCUSSION

Considering the difficulties involved in determining nutrient availability to algae through chemical analyses of water samples and the favorable results obtained in the present investigation in evaluating nitrogen and phosphorus supplies from the concentrations of these elements in the algal cells, the earlier optimism regarding the latter procedure (Gerloff and Skoog 1954) and its value in developing methods of bloom control seems justified.

Several aspects of the procedure followed might be questioned, however. In the first place, results have been presented only for one organism, *Microcystis aeruginosa*, and work might profitably be extended to additional species. It should be pointed out, however, that laboratory studies with other bloom-producing blue-green algae have shown them to have relatively the same quantitative requirements for the essential elements as does *Microcystis*.

Mention also should be made of the necessity of obtaining clean samples of the test organism, not only free from other particles and organisms, but also with a minimum of inert surface deposits. The presence of encrustations or precipitates might introduce errors if they contain unavailable deposits of the test element. This of course would be more apt to happen with phosphorus than with nitrogen and might give misleadingly high phosphorus content values. Although this possible source of error is not excluded, its significance is minimized by the fact that other evidence (lake water enrichment experiments, etc.) points to the nitrogen supply as more critical than that of phosphorus or other elements.

A more subtle manner in which the level of phosphorus might be limiting the growth of *Microcystis* in a lake would be through an indirect influence on the nitrogen supply. For example, it is

considered that nitrogen-fixing organisms have a rather high phosphorus requirement. Conceivably, therefore, fertilizing with phosphorus might lead to an increased nitrogen supply and thus to increased growth of the algae even when the existing phosphorus level already was higher than would seem to be required.

Similar complex biological interactions, in addition to more direct physical-chemical antagonisms and chelation phenomena, might exist with respect to some other elements. Nevertheless, considering the enormous complexity of hydrobiological phenomena, the reproducibility of the results and agreement in conclusions from different experimental approaches in pointing to the critical role of the nitrogen supply is striking. This is not to minimize the possible importance of other prerequisite factors, temperature, light, etc., for growth of algae. It also is obvious that the results obtained here can be applied to other lakes only to the extent that general conditions, for example fertility, are similar.

SUMMARY

The relative requirements and availability of nitrogen and phosphorus for growth of *Microcystis aeruginosa* in southern Wisconsin lakes has been evaluated by (1) comparisons of *Microcystis* growth in sterilized lake water enriched with nitrogen, phosphorus, and other essential elements singly and in various combinations; (2) by comparisons of minimum nitrogen and phosphorus requirements of *Microcystis* as determined in laboratory culture experiments with the quantities of these elements present in lake water; and (3) by comparisons of cell contents of nitrogen and phosphorus in *Microcystis* collected from lake blooms with "critical levels" (minimum cell contents required for maximum growth) established in the laboratory. The critical levels of the nutrients are to some extent a function of the carbohydrate content of the algae cells, and a procedure is presented for adjusting the percentage nitrogen content in accordance with the total carbohydrate content.

Cell content comparisons showed that in all cases nitrogen supply was close to limiting and in several instances had become limiting for growth. All results indicated nitrogen to be present in far less abundant supply relative to need than phosphorus.

The practical implications of the results and the possible usefulness of the methods with reference to control of bloom production by removal of nitrogen or eventually other limiting nutrients from pollution sources are discussed briefly.

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FACTORS INFLUENCING VARIATIONS IN POPULATIONS OF *ANOPHELES QUADRIMACULATUS* IN SOUTHWESTERN GEORGIA

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The analyses reported in this paper were undertaken to appraise the effect of some environmental factors on populations of adult *Anopheles quadrimaculatus* Say in southwestern Georgia. Measurements of *Anopheles* densities were made during the period 1939 through 1952 as part of a study on the natural history of malaria in a representative endemic area (Bradley and Goodwin 1949; Goodwin 1950). Concurrent observations were made of pertinent ecologic conditions as described in previous reports (Hendricks and Goodwin 1952a, 1952b) and attempts were made periodically to correlate these data and to delineate causal association between various environmental conditions and abundance of *A. quadrimaculatus*. Since a multiplicity of variable factors affect production and longevity of this mosquito, no precise consistent relationships were apparent from these analyses. These studies did show, however, that temperature of water in the mosquito breeding areas studied was a critical limiting factor in mosquito production and was related closely to variations in numbers of adult *A. quadrimaculatus* in the resting places observed regularly. This report presents some results of these analyses and indicates some relations between variations in surface-water temperatures and populations of *A. quadrimaculatus*.

PROCEDURES

Observations were made in portions of Baker and Early Counties in southwestern Georgia from 1939 through 1952. The general area and the specific ponds studied were described in detail by Hendricks and Goodwin (1952a).

When observations were commenced, one objective was to obtain qualitative data on seasonal and annual changes in density of the malaria vector. Collections of adult *Anopheles* were made from the types of diurnal resting places—houses, barns, and hollow trees—usually inspected in routine measurement of anophelism. Since data from these sources do not permit reliable quantitative analysis, an attempt was made to devise an artificial diurnal shelter for mosquitoes that would enable comparable enumeration of adult *Anopheles*. A 1-foot cubical wooden box painted red inside and out was found to be most practical, though not ideal, for this purpose (Goodwin 1942). These boxes were intrinsically comparable but were not similarly attractive to *A. quadrimaculatus* because of variations in the potential attractiveness of locations in which they were placed. Boxes were nailed to trees in shaded locations near breeding places of *A. quadrimaculatus* with the bottoms of the boxes about 4 feet from the ground. The boxes were inspected, usually at

weekly intervals, and mosquitoes in the boxes counted and identified. Data used in this report were collected in this manner from 1943 through 1952 in the environs of Mossy, Springfield, and Putney Ponds, which were favorable for production of *A. quadrimaculatus*. (See Hendricks and Goodwin, 1952a, for complete descriptions.)

Mosquito production and variations in numbers of *Anopheles* in the vicinity of these ponds were generally representative of all the areas studied. The number of stations inspected at each pond varied from year to year but some boxes were examined regularly throughout the years of observations. Inevitably there were breaks in the data due to inclement weather or to disturbance or removal of a box. Only data obtained from collecting stations within 50 feet of the breeding area were used for this analysis. Previous studies in the area have shown that mosquitoes disperse rapidly from breeding places and that samples of population at breeding places appear to be as representative of the areal population as are collections made at other locations in the region (Goodwin 1949).

Records of air and surface-water temperatures, rainfall, pond levels, and ground-water levels were

obtained with recording instruments according to procedures described previously (Hendricks and Goodwin 1952a, 1952b).

For purposes of analyses, data on populations of adult mosquitoes for the representative years 1946, 1947, and 1948 were arranged graphically to show the actual number of adult *A. quadrimaculatus* collected on each day, the percent of the annual catch taken in each collection, and a 4-week moving average of total adults collected. Each expression of *Anopheles* density was compared with data on each of the climatic factors measured during the same period. Data on surface-water temperatures were not obtained during 1943 and 1944. Since populations of *A. quadrimaculatus* were very large during this period and comparison of density with pertinent physical factors was desirable, surface-water temperatures were computed using the formula given for Mossy Pond by Hendricks and Goodwin (1952b).

RESULTS AND DISCUSSION

Reliability of sampling procedures

Figure 1 shows the total weekly counts of *A. quadrimaculatus* in 5 boxes inspected regularly

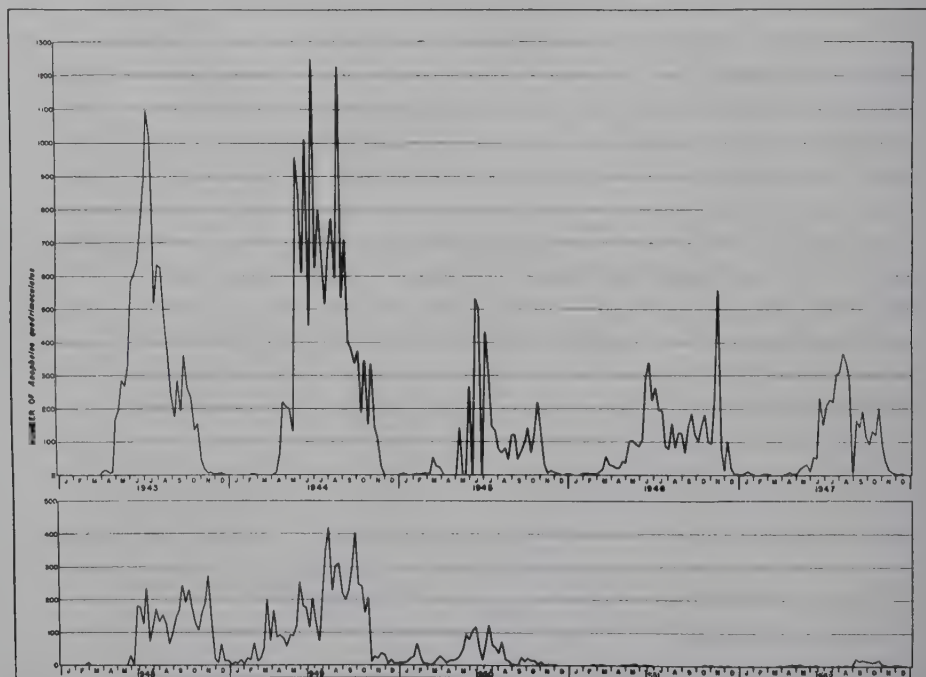


FIG. 1. Number of adult *Anopheles quadrimaculatus* collected weekly from index stations at Mossy Pond, Baker County, Georgia, 1943 through 1952.

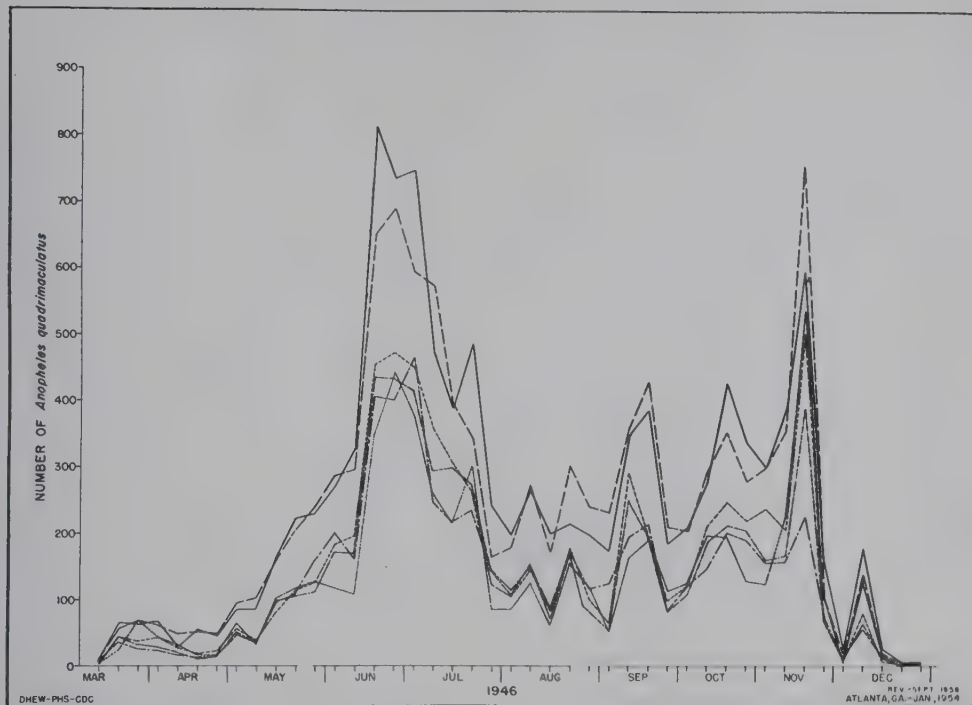


FIG. 2. Number of *Anopheles quadrimaculatus* collected weekly during 1946 in 6 series of stations at Mossy Pond, Baker County, Georgia.

during the entire period of observation at Mossy Pond, the most prolific breeding place studied.

Since the only criterion of selecting these stations was the continuity of record, tests were made to determine if numerical variations in collections of mosquitoes in this series of stations corresponded with variations of other series selected on other bases. Two series of 10 stations and 4 series of 5 stations were selected by drawing at random slips of paper each marked with a number of 1 of the 22 stations inspected at Mossy Pond during 1946. Figure 2 shows the total number of adult *A. quadrimaculatus* collected weekly in each series of stations. The similarity of variations shown by these 6 series and the series used in Figure 1 indicates that the 5 index stations selected are as reliable as any other series as indicators of variations in populations of adult *A. quadrimaculatus*.

Variations of populations at different breeding places. Measurements of adult *A. quadrimaculatus* in the environs of different breeding areas indicate that appearance of the first spring brood and disappearance of adult *Anopheles* in the fall occur at approximately the same time at breeding

places affected by the same general climatic conditions. Intraseasonal variations in local populations, however, are not necessarily similar at all ponds in the same general area.

Some extreme climatic factors such as adverse high and low atmospheric temperature, torrential rain, and winds of high velocity exert a general regional influence which is detected uniformly in measurement of *Anopheles* density throughout the area. Generally, however, intraseasonal variations in populations result from local influences and not from conditions that have a uniform effect over the entire region. Figure 3 indicates the total weekly counts of *A. quadrimaculatus* adults collected during 1946 from the 5 index stations at Mossy Pond, 7 at Springfield Pond, and 8 at Putney Pond. The latter ponds are approximately 12 miles from Mossy Pond in opposite directions. The seasonal trends of population at these 3 breeding places are essentially similar but the simultaneous occurrence of high and low counts is largely coincidental.

The dissimilarity of variations at the different breeding places is probably attributable to difference in local conditions that affect production or

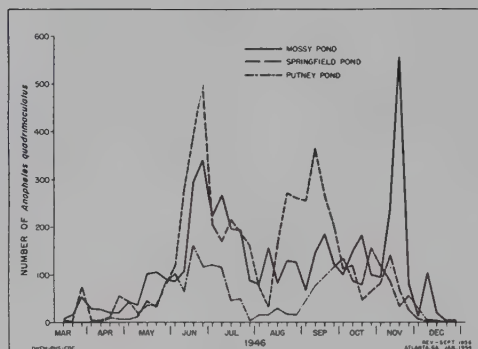


FIG. 3. Number of *Anopheles quadrimaculatus* collected weekly during 1946 from 5 index stations at Mossy Pond, 7 at Springfield Pond, and 8 at Putney Pond, Baker County, Georgia.

longevity of *Anopheles*. The analyses described subsequently were designed to determine if local fluctuation in populations could be related to measurable environmental factors. Since data from Mossy Pond and Springfield Pond are more substantial than those from Putney Pond, information from the latter area is not considered further in these analyses.

Influence of climatic factors

Precipitation. The cumulative weekly rainfall and the weekly maximum and minimum air temperatures at Mossy Pond are shown in Figure 4. Comparison of weekly precipitation and variations in numbers of *A. quadrimaculatus* (Fig. 1) indicated no obvious correlation. There was likewise no consistent relationship between number of rainy days, daily distribution of precipitation, or total rainfall and variation in number of *A. quadrimaculatus* either during the breeding season or between different seasons. Populations obviously were higher when rainfall was sufficient to maintain water in breeding areas at the levels conducive to the development of a favorable biologic balance throughout the years; these long-term relationships were considered in previous studies (Hendricks and Goodwin 1952a). Variations within a breeding season, however, apparently were not affected directly by the amount or distribution of rainfall.

Pond elevations. The principal breeding places of *A. quadrimaculatus* in the area studied are heavily vegetated limesink ponds. Although production of *A. quadrimaculatus* obviously requires suitable habitat for development of the aquatic stages, consistent quantitative relationships could not be detected between seasonal variations in

density of population and area of water surface or volume of water in a pond. Field workers recognize that conditions suitable for development of *A. quadrimaculatus* may occur over a wide range of stages or at several different levels in a pond. Although direct quantitative relationship is usually apparent between regional mosquito populations and extent of water surface, a similar correlation cannot necessarily be anticipated at individual breeding areas. Many breeding places provide conditions more favorable for production of *A. quadrimaculatus* when the water level is high than when it is low; probably as many breeding places have a converse relationship. The determining ecologic factor, within limits of favorable chemical conditions, is probably the amount and type of vegetation. This association has been elaborated by Hess and Hall (1943).

Temperature. Probably more analyses have been concerned with the effect of temperature on development and behavior of animals, including mosquitoes, than with any other environmental factor. Attempts have been made in many instances to make precise statistical analyses of these relationships and in some cases correlations have been demonstrated with a high degree of statistical validity. Hurlbut (1943) and Hufaker (1944), for example, have studied the relation of temperature to the rate of growth of *A. quadrimaculatus* and Barr (1952) investigated the resistance of this species to heat. Bates (1949) and Thompson (1951) have provided summaries of information on the behavior of mosquitoes in relation to temperature and other factors. With the present data, precise correlation analyses did not appear advisable, partly because of the inherent difference in accuracy of measurement of climatic factors and mosquito populations, and, as illustrated subsequently, no single expression of temperature, e.g., maximum, minimum or mean, enables explanation of all of the variation observed in populations of *A. quadrimaculatus*. In view of the variety of conditions known to affect populations of mosquitoes, detection of a close correlation between one factor, or a limited number of factors, would not necessarily identify a principal causative factor. In the indications of relationship which follow attention has been given to the possibility of influence of other factors and to the possibility that relationships may be due to other factors that affect both variables under consideration.

Study of Figures 1 and 4 shows that variations in both temperature and mosquito counts are inconsistent from week to week with respect to upward or downward trend. A comparison of week-

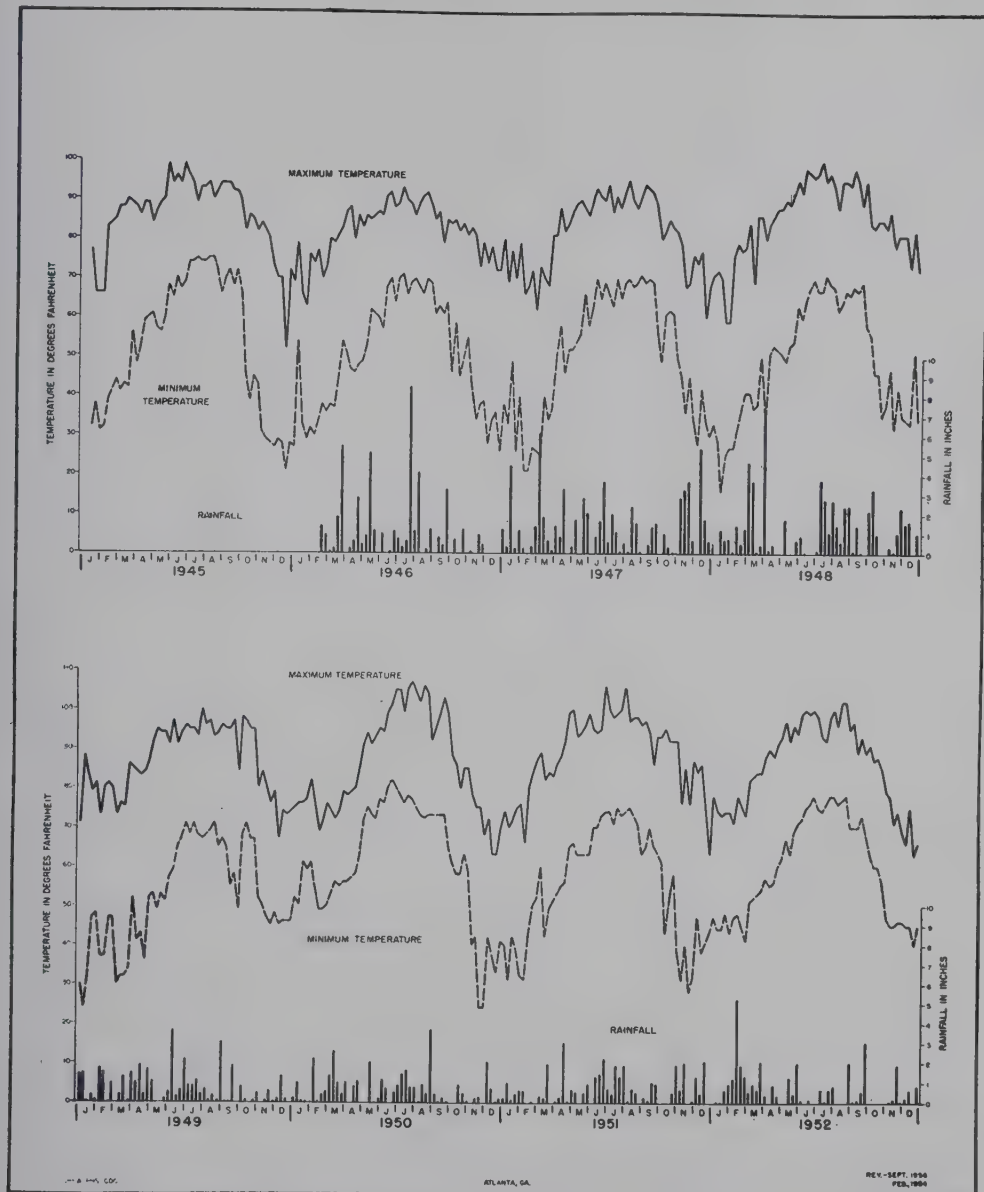


FIG. 4. Weekly rainfall, maximum and minimum air temperature at Mossy Pond, Baker County, Georgia, 1945 to 1952.

ly measurement shown in these figures indicates no consistent correlation with respect to either trend or magnitude of change. The data for temperature (Fig. 4) are not necessarily shown for the day on which mosquitoes were collected (Fig. 1); but the relation between data obtained on the same day showed similar relationships. To provide statistics that are suitable for comparison,

data on both temperature and mosquito density were smoothed by calculation of moving averages. It was determined that a 4-week moving average of mosquito counts provided a smooth indication of trends in abundance. Other considerations, indicated below, affected the selection of this interval for the temperature data.

The density of mosquitoes on a specific day is

determined in part by the cumulative effect of climatic conditions during the life span of individuals that comprise the extant population. Also, the number of individuals in a population is limited by the size of previous populations. To provide some expression of temperature that would be generally comparable with measurements of mosquito density, computations were made of 28-day moving averages of mean measurements of air temperature. This period was selected because the average duration of larval development is about 2 weeks and the approximate longevity of adult mosquitoes in nature is probably also about 2 weeks. Although selection of the 28-day interval was arbitrary, tests showed that calculations based on shorter intervals provided statistics that afforded inferior correlations. Since calculations based on the 28-day interval provided data that were closely correlated with variation in mosquito density, no advantages were apparent in using longer intervals that would further smooth the temperature measurements. Variations in numbers of *A. quadrimaculatus* and fluctuations of 28-day moving averages of air temperature were generally similar, although consistent correlations could not be demonstrated at the breeding areas considered (Mossy and Springfield Ponds).

Variations in both air and water temperatures were closely related to variations in density of mosquitoes. Water temperatures, however, were more consistently associated with differences between counts at different breeding areas. During September 1946, for example, *A. quadrimaculatus* counts at Springfield Pond were increasing while counts at Mossy Pond were decreasing. This difference of direction is not attributable to air temperature since air temperature as measured in this study is generally the same over a wide area. Water temperatures, however, are subject to variations in different environments depending on a variety of ecologic conditions. Previous studies have shown that air and surface-water temperatures usually fluctuate together since generally the same factors affect both. Although the relationships between air and surface-water temperatures are not causal, mathematical relationships between them can be determined. These relationships are constant as long as gross physical and biological features of the pond are stable (Hendricks and Godwin 1952b). The magnitude and direction of differences between water temperature in a pond and air temperature in environs of the pond depend upon local environmental factors.

Springfield Pond, for example, is a small pond approximately $\frac{1}{2}$ acre in area. The pond basin is shaded almost constantly through the day by

a dense growth of black gum (*Nyssa sylvatica biflora*). During the growing season a dense covering of various floating and emergent plants almost completely obscures the water surface. The maximum depth of water is approximately 2 feet at the center of the circular basin and decreases uniformly to the edges. Little direct sunlight reaches the water surface and heating due to radiation is slight. Mossy Pond covers approximately 15 acres, and contains proportionately less vegetation; this pond, consequently, receives more direct solar radiation. The comparatively small volume of water in Springfield Pond enables more sensitive response to conditions that affect water temperature. Consequently, during the mosquito breeding season mean surface-water temperatures are consistently 3 to 5 degrees higher at Mossy Pond than at Springfield Pond.

The 28-day moving averages of surface-water temperatures and 4-week moving averages of adult *A. quadrimaculatus* count at Springfield and Mossy Ponds for 1946, 1947, and 1948 are shown in Figure 5. These graphs indicate a close similarity in the direction and magnitude of variations in surface-water temperature and counts of *A. quadrimaculatus* expressed as moving averages covering the same interval. Variations in numbers of these mosquitoes can be explained on the basis of changes in temperature of the water surface, as indicated by the following examples from several years of record.

In 1946 adult *A. quadrimaculatus* were detected in the environs of both Springfield and Mossy Ponds at about the same time (Fig. 5). Subsequently, water temperatures were higher in Mossy Pond and adult *A. quadrimaculatus* increased faster than at Springfield Pond. Peaks of populations at both ponds were reached early in July.

The subsequent precipitous drop in numbers of adult mosquitoes is attributable to the mortality of both larval and adult *Anopheles* caused by high air and water temperatures (Love and Whelchel 1957). Occurrence of air temperatures above 95° F was invariably accompanied by depression in numbers of adult *A. quadrimaculatus*. Concurrent water temperatures were also correspondingly high but the magnitude of these maxima is obscured by the use of moving averages. The average measurements are satisfactory for indicating trends within the range of tolerance of the organism but the limiting effect of extreme conditions must be considered in evaluating the relation of causal factors. From July 7 to 15, the air temperatures reached 95° or above every day except one. Where temperatures moderated, the number of adult *A. quadri-*

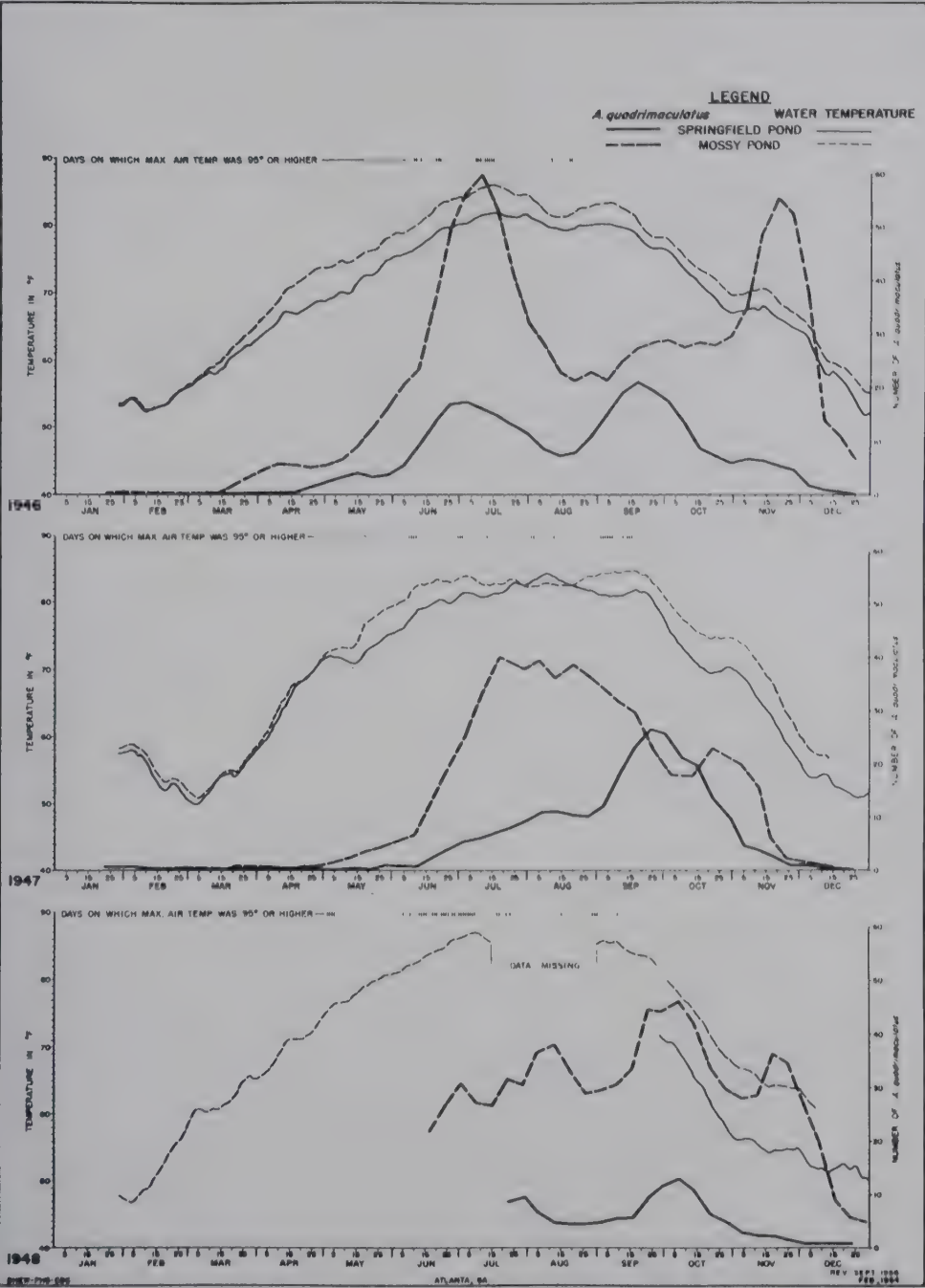


FIG. 5. Twenty eight-day moving averages of water temperature and 4-week moving averages of adult *A. quadrimaculatus* counts from Springfield and Mossy Ponds, Baker County, Georgia, 1946-1947-1948.

maculatus in resting stations increased and a definite upward trend was evident by early September.

Water temperatures that accompany sustained air temperatures above 95° F are detrimental to the larval stages and are probably responsible for appreciable mortality (Goodwin and Love 1956). The earlier recovery of *A. quadrimaculatus* population in the environs of Springfield Pond than at Mossy Pond is attributable to the more rapid re-establishment of favorable conditions of temperature.

Comparison of adult counts during October at the two ponds again illustrates the necessity for considering the extremes that limit development. The graphs of surface-water temperatures in Figure 5 show that mean temperatures were receding uniformly and that the average temperature at Mossy Pond was only 2° higher than at Springfield Pond. Concurrently, the number of adult *A. quadrimaculatus* was increasing at Mossy Pond and decreasing at Springfield Pond. During October, the mean extreme surface-water temperatures at Springfield Pond were 71.5 and 62.1° F. Since larval development proceeds slowly within this range (Goodwin and Love 1956), the adult population would not be replenished in numbers sufficient to maintain the population. During the same month, corresponding temperatures at Mossy Pond were 80.6 and 63.5° F. Within this range, temperatures are sufficiently high to accelerate larval production and to maintain the adult population. In early November the slight rise in temperature was sufficient to effect an increase in the number of adult *A. quadrimaculatus* in the resting stations under observation. This increase was noted at Springfield as well as Mossy Pond but the magnitude of change was much greater at the former location. Increase in numbers of mosquitoes in the resting places examined probably is not due entirely to acceleration of larval development. During cooler weather, *A. quadrimaculatus* in the area of this study leave the comparatively exposed shelters which are frequented in the warm seasons and occupy more occult shelters which afford more protection (Zukel 1949). During intermittent warm periods, however, the numbers of mosquitoes increase in the normal estival shelters as the quiescent individuals in the winter resting places resume activity.

The same relationships are apparent in data for 1946 and 1947. Detrimental high temperatures occurred earlier in 1947 and were sustained for a longer time than in the previous year. This resulted in suppression of the peak of population and frequent recurrence of high temperature prevented recovery of the population during July

and August. Early in September 1947 high temperature on several consecutive days caused a drop in numbers of *A. quadrimaculatus* similar to that observed in June 1946.

The rate of decline in 1947 was not as precipitous, however, as in 1946 and at Springfield Pond high air temperatures apparently did not prevent the population reaching the height of the previous year. Excessively high water temperatures at Springfield Pond in July and August 1947 prevented seasonal increase in the local population comparable with the population at Mossy Pond. Late in August, however, conditions were more favorable and a peak was reached comparable to the maximum density during the previous year. The difference in direction of population trends at Mossy and Springfield Ponds during August and September 1947 was probably affected significantly by water temperature. On 14 days, between September 1 and 20, the maximum water-surface temperature exceeded 93° F. Mean extreme temperatures during this period were 93.0 and 77.2° F and the maximum temperature was 98° F. An increase in *A. quadrimaculatus* occurred at Mossy Pond when more favorable conditions of temperature developed late in October. A similar depression attributable to high water temperatures did not occur at Springfield Pond during the same period. Mean extreme water temperatures at this pond were 88.2 and 74.0° F and the maximum which occurred only once was 93.0°.

Data for 1948 are incomplete but corroborate relations between temperature and *A. quadrimaculatus* populations observed in 1946 and 1947. Extremely high temperatures during the summer months suppressed development until favorable conditions occurred early in October. An increase in numbers of adult *A. quadrimaculatus* was observed in mid-November 1948 which was probably due, in part at least, to the factors responsible for similar increases in November 1946 and October 1947. As water temperatures became lower in the fall, the period of larval development increased and larvae temporarily became more abundant in breeding places. Apparently favorable conditions of temperature recurred before lethal low temperature reduced the number of larvae, the development of the retarded larvae was accelerated and unusually high proportions of the aquatic stages produced larvae within a short period.

The highest populations of *A. quadrimaculatus* observed in this study occurred in 1943 and 1944. Since data on water temperature were not available for these years, computations were made

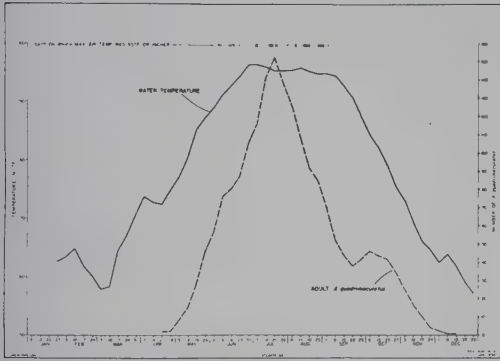


FIG. 6. Twenty-eight-day moving averages of computed water temperatures and 4-week moving averages of adult *A. quadrimaculatus* counts at Mossy Pond, Baker County, Georgia, 1943.

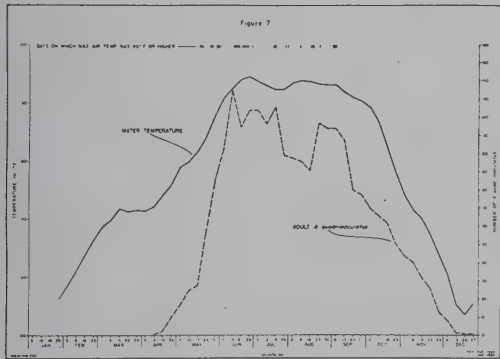


FIG. 7. Twenty-eight-day moving averages of computed water temperatures and 4-week moving averages of adult *A. quadrimaculatus* counts at Mossy Pond, Baker County, Georgia, 1944.

using the formula given by Hendricks and Goodwin (1952b). Moving averages of the computed water temperatures and of *A. quadrimaculatus* counts are shown in Figures 6 and 7 in the same manner that data of other years are illustrated in Figure 5. Although the calculated data do not show the close conformity as those from direct observations, the same relations are apparent between temperature and abundance of adult *A. quadrimaculatus* in the resting places examined. Calculated temperatures were considerably higher than any water temperatures observed in this study. During 1943 air temperatures above 95° F did not occur until June and the number of *A. quadrimaculatus* observed in shelters increased steadily until the end of that month. In 1944, however, such high temperature occurred approximately a month earlier and the population was apparently suppressed earlier, even though seasonal

production of *A. quadrimaculatus* started at the same time in both years. In 1944 the maximum air temperature was 95° F or higher on 7 days in May and 18 days in June; in May 1943 air temperatures did not reach 95° F, and in June such temperatures occurred on only 9 days. In 1943 the precipitous drop in numbers after the peak was reached is attributable to the severe conditions of temperature experienced in late August and early September. High temperatures were intermittent during 1944 and populations were sustained at relatively higher levels than in 1943.

SUMMARY

Measurements were made of *A. quadrimaculatus* abundance and of precipitation, air temperature, water-surface temperature, pond stages, and other physical factors in southwestern Georgia. With the methods employed, no consistent direct correlations were apparent between variations in numbers of *A. quadrimaculatus* and changes in the climatic conditions observed. Since the population under observation was affected by environmental conditions through the life of individuals comprising the population, measurements expressed as moving averages were compared. Temperature of the water surface in breeding places was found to be closely associated with intra-seasonal variations in populations of *A. quadrimaculatus*. Percipitous decreases in numbers of mosquitoes were attributable to extremely high air temperatures, above 95° F.

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LETHAL EFFECTS OF HIGH TEMPERATURES ON THE IMMATURE STAGES OF *ANOPHELES QUADRIMACULATUS*

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INTRODUCTION

Previous ecologic studies of *Anopheles quadrimaculatus* Say in southwestern Georgia indicate a close correlation between adult *A. quadrimaculatus* populations and surface-water temperatures in the breeding places (Goodwin and Love 1957). This correlation suggests that high temperatures are detrimental to the development of the immature stages of *A. quadrimaculatus*; adult populations were always reduced during periods of highest surface-water temperatures.

The present report gives results of laboratory experiments designed to evaluate the interpretations made from field observations by determining the quantitative relationships between mortality of *A. quadrimaculatus* larvae and pupae and surface-water temperatures.

Previous studies of the effects of temperature on *Anopheles* larvae have been made. Hurlbut (1943) and Huffaker (1944) reported on the correlation between various moderate temperatures and time of larval development for *A. quadrimaculatus*. Barr (1952) demonstrated that *A. quadrimaculatus*, *A. freeborni*, and *A. astecus* vary in their ability to withstand a temperature of 42° C, and also that, within each of these species, resistance to this high temperature is lessened as the larvae grow older.

MATERIALS AND METHODS

Laboratory Studies

In preliminary tests to determine if differences occurred in rates of development and survival between colonized and wild *A. quadrimaculatus*, larvae of both strains were reared simultaneously

at constant temperatures. Experiments were conducted at various constant temperatures from 55 to 90° F. Colonized mosquitoes were the Q₁ strain of *A. quadrimaculatus* maintained in the station insectary. Wild mosquitoes were reared from eggs deposited by gravid female *A. quadrimaculatus* collected from adult resting stations in the field. Ova were obtained in enamel pans containing approximately one-half inch of water, which were left overnight in the cages of mosquitoes. Unless ova were to be used for special studies, they were allowed to hatch and the larvae reared in the insectary at temperatures varying from 83 to 87° F. For rearing at constant temperature, ova were counted into 3-inch finger bowls or enamel pans, and the container placed in a constant-temperature water bath.

When larvae were used in a study, specimens at the same stage of development were selected at random from several of the pans containing larvae which were being reared in the larval room of the insectary. This method of selection gave a representative sample of the larvae of various ages of the instar under study. No effort was made to select larvae of a precise age measured in number of days.

Exposures to high temperature were made by placing the larvae in a circular enamel pan 8 inches in diameter. Water was maintained at a depth of approximately 2 inches. The pan was floated in an oil bath 9 inches in diameter. Heat was applied to the oil bath with a Bunsen burner. With this arrangement water temperature could be maintained within $\pm .5^\circ$ F by regulating the size of the flame. Measurements of temperature us-

ing a bead-type thermistor sensing element indicated that temperatures throughout the water bath varied less than .05° F. Sufficient preliminary tests were made to show that no detrimental effects resulted from oil fumes.

Exposures to Constant High Temperatures. In the first series of tests at high temperature, 10 or 25 larvae were placed in small latern chimneys (3 inches tall by 2 inches in diameter) which were covered on the bottom with several thicknesses of cheesecloth. These chimneys were placed in finger bowls that contained water to a depth of approximately 1 inch. The chimneys were transferred five at a time to the water bath when the desired temperature was reached. The chimneys were then removed from the bath one at a time at uniform intervals and returned to the finger bowls. Larvae were then removed from the chimneys, placed in the finger bowls, and fed lightly. After 24 hours, mortality was determined. Larvae which failed to move when touched lightly with a pipette were recorded as dead. At least 6 replicates involving a minimum of 150 larvae were used for each test. Larvae of each instar, and pupae, were exposed in this manner to temperature intervals of approximately five degrees from 105 to 125° F. Times of exposure at each temperature were varied and the 50-percent endpoint computed according to the method given by Reed and Muench (1938).

Exposures to Fluctuating High Temperatures. A second series of tests was made in which the possible shock caused by sudden temperature change was eliminated. Larvae in their chimney containers were placed in the oil and water bath at room temperature and the temperature raised slowly to the desired level. After exposure, heat was removed and the water allowed to cool. When the temperature dropped below 100° F, the chimneys were removed to finger bowls containing well water at approximately the same temperature, fed lightly, and held for 24 hours before checking mortality. As in the previous series of tests, five containers were placed together in the bath. In this instance, all stages from first-instar larvae to pupae were used in each test. Specimens in a single container were all in the same stage of development. Twelve tests made in this manner were sufficient to show the relative resistance of the different stages and to compare the effects of gradual and rapid temperature changes on mortality.

Exposures to Simulated Natural Temperatures. Two tests were run in which temperatures recorded from a mosquito-breeding area in nature

were simulated in a controlled temperature water bath. The heating and cooling equipment in the bath was controlled by time switches which could be set 24 hours in advance. Ova were counted into pans and placed in the bath on the morning after oviposition. Larvae which hatched were observed daily for development and mortality. With each of these tests control series of larvae were reared at constant temperatures of 70, 85, and 90° F.

Field Studies

Field measurements used in this study were made in 1943. Weekly collections of 30 dips with 9 by 14-inch enamel pan were made in the same portion of a prolific mosquito-breeding area in southwestern Georgia (Mossy Pond). A four-week moving average of the total number of fourth-instar *A. quadrimaculatus* larvae was compared with a four-week moving average of weekly maximum air temperatures. Moving averages of the data were used since temperatures which occur at any time during the period of larval development could affect the number of specimens present at any particular time. Also, trends of fluctuation in population and temperatures show more clearly when moving averages are used.

Water temperatures were not available for this particular year, but since consistent close correlations between surface-water temperatures and air temperatures have been demonstrated (Hendricks and Goodwin 1952), the air temperature may be used to show relationships between larval populations and temperature variations.

RESULTS

Laboratory Studies

The rates of survival and development of the colonized and the wild *A. quadrimaculatus* were studied at relatively constant temperatures (Table I). At temperatures between 55 and 60° F, the time of development from ova to adult was between 57 and 64 days, but only 1 percent of ova from both strains produced adult mosquitoes. At temperatures of 70 and 75° F, 41 percent of the colonized specimens and 43 percent of the wild specimens survived. Adults were first obtained from both strains in 18 days. At temperatures between 85 and 90° F, survival was 51 and 55 percent for the colonized and wild specimens, respectively, and adults were first obtained in 11 days. Because these results indicated that there were no significant differences in development and survival of the two strains under the conditions used, subsequent tests were conducted with only the colonized strain.

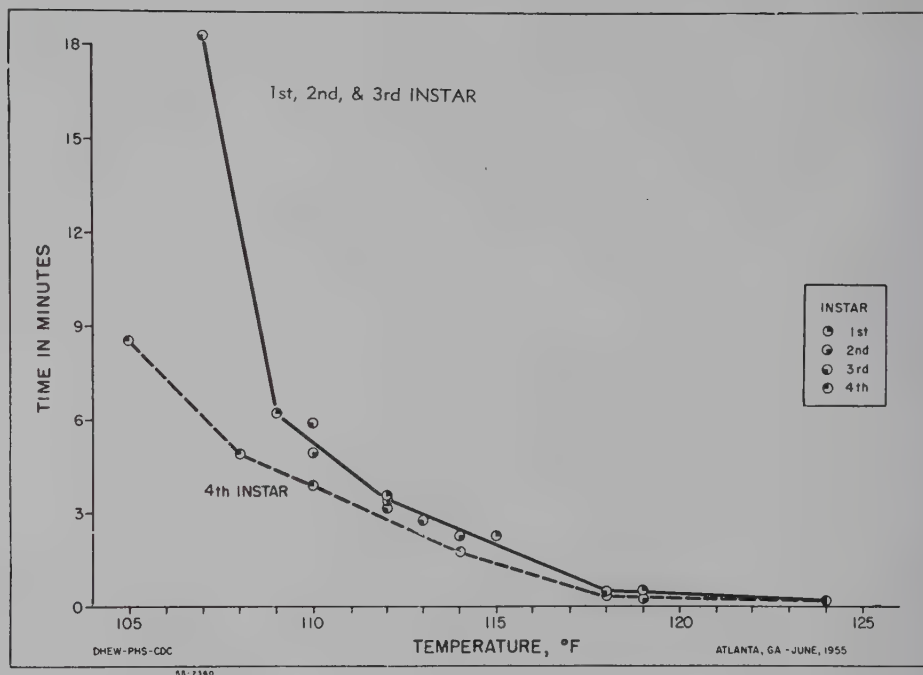


FIG. 1. Relation of time of exposure to mortality of *Anopheles quadrimaculatus* larvae subjected to rapid increases in temperature.

TABLE I. Comparison of survival and time of development of wild-caught and colonized *A. quadrimaculatus* larvae reared at a constant temperature from 55 to 90 degrees F

Degrees F	COLONIZED <i>A. quadrimaculatus</i>			WILD <i>A. quadrimaculatus</i>		
	Number of specimens	Percent survival	Time of development (days)	Number of specimens	Percent survival	Time of development (days)
55 - 60....	644	1	58 - 62	1,000	1	57 - 64
70 - 75....	1,300	41	18	1,750	43	18
85 - 90....	1,300	51	11	600	55	11

In all tests, fourth-instar larvae were found to be less resistant to high temperature than were other stages. Third-, second-, and first-instar larvae were progressively more resistant, but the differences between these three stages were not great.

Exposures to Constant High Temperatures. When temperatures were raised suddenly to 105° F or higher, 50 percent of *A. quadrimaculatus* larvae were killed by short exposures (Fig. 1). At 105° F, 50 percent of fourth-instar larvae were killed in 8 minutes and 32 seconds, and at 108° F, 50 percent of fourths were killed in 4 minutes and 55 seconds. At 118° F, only 18 seconds were

necessary to kill 50 percent of fourth-instar larvae, and at 124° F, exposures of less than 3 seconds resulted in 50 percent or greater mortality.

First-, second-, and third-instar larvae are shown by a single line in Figure 1 since differences in resistance were slight. At 107° F, 50 percent of third-instar larvae were killed by an exposure

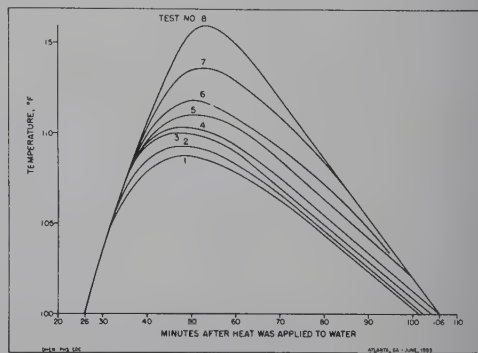


FIG. 2. Rate of changes in temperature of water in tests to determine mortality of *Anopheles quadrimaculatus* larvae produced by gradual increases in temperature.

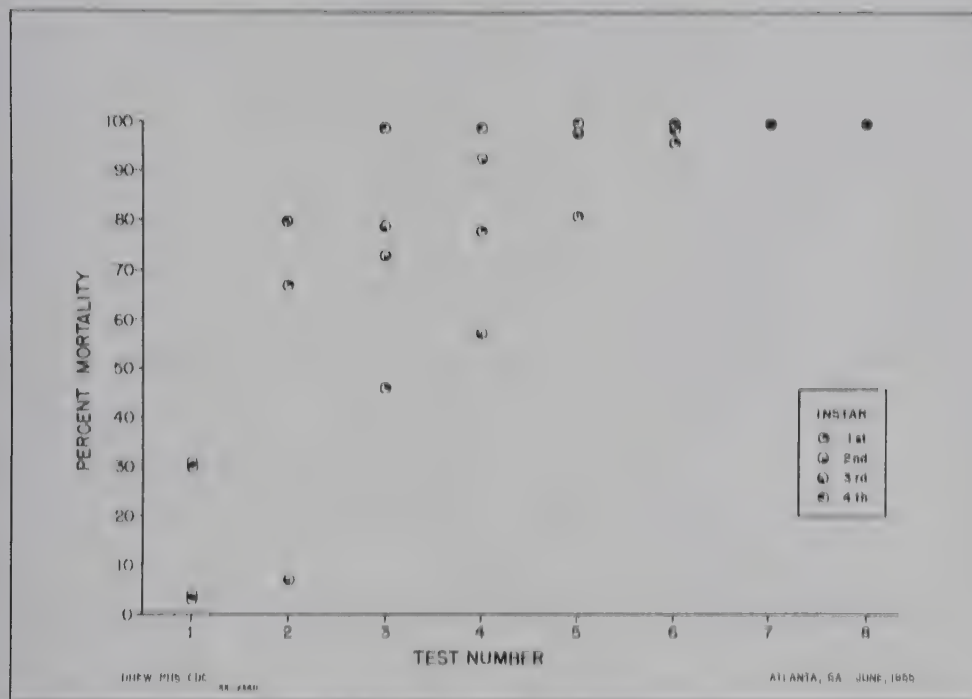


FIG. 3. Percent mortality of *Anopheles quadrimaculatus* larvae subjected to temperatures shown in Figure 2

of 18 minutes and 20 seconds; at 109° F, 50 percent of first-instar larvae were killed by an exposure of 6 minutes and 15 seconds; and at 110° F, 50 percent of second-instar larvae were killed by an exposure of 4 minutes and 55 seconds. Above 110° F, the differences in resistance were not as striking, but fourth-instar larvae were still less resistant than were the younger instars.

Exposures to Fluctuating High Temperatures. When temperatures were raised slowly, the rate of mortality was not unusually high until the maximum temperature exceeded 109° F. Figure 2 shows the course of temperatures in 8 of the 12 tests, and Figure 3 shows the resulting mortality in each of these tests. Only 8 tests are included in these figures because the remaining 4 were almost exact duplicates of some of those shown. In test 1 (Figs. 2 and 3), the temperature was above 100° F for 75 minutes and above 105° F for 45 minutes. Mortality in this test was 3, 31, 4, and 30 percent of the first-, second-, third-, and fourth-instar larvae, respectively. The maximum temperature in this test exceeded 108.5° F, but did not reach 109° F. In test 3, mortality of first-, second-, third-, and fourth-instar larvae was 46, 73, 79, and 99 percent, respectively. These larvae were exposed to a temperature above 100° F

for 78 minutes, above 105° F for 48 minutes, and above 107° F for 35 minutes. In other tests, mortality was almost complete when the temperatures were allowed to rise to 111° F or above.

The measurements of lethal effects of temperature on pupae were considerably more difficult than with larvae. Usually pupae could be induced to move 24 hours after exposure to higher temperatures, but very few adults emerged from the exposed pupae (Table II). In test 1 (Fig. 2 and Table II), 24-hour pupal mortality was only

TABLE II. Percent mortality of pupae 24 hours after exposure to high temperature and percent of *A. quadrimaculatus* adults which emerged from tested pupae

Test	Maximum temperature	Per cent mortality after 24 hours	Per cent emerged
8*	116	100	
7	114	100	
6	112	87	2
5	111	83	
4	110.5	82	
3	110	34	
2	109.5	27	
1	109	14	6
Control		5	92

*Test numbers refer to Figure 2 where complete temperature data are given

14 percent, but only 6 percent of the specimens produced live adults. In the 7 other tests shown, the 24-hour pupal mortality ranged from 27 percent to 100 percent, but only 2 adults were obtained from the 700 pupae exposed.

Exposures to Simulated Natural Temperatures. The effect on pupae exposed to high temperature was consistent in all tests, including those in which water temperature was varied to correspond to conditions observed in nature. In one test that simulated conditions found in Mossy Pond from May 24 to June 8, 1947, the average water temperature for the entire developmental period was 83.8° F. The temperature reached 100° F on 7 days and was held at 100° F or above for a total of 27 hours. The maximum temperature was 103° F, which occurred while the larvae were still in the first instar. In this test, larval mortality was consistently about 2 percent per day throughout the period of larval development. However, 57 percent of the specimens pupated and each pupae produced a vigorous adult. In a second test which simulated natural Mossy Pond water-temperature fluctuations from May 10 to 25, 1947, the average temperature throughout the test was 84.8° F. The temperature reached 100° F on 8 days and was held at 100° F or above for a total of 44 hours. In this test, too, larval mortality was approximately 2 percent per day, and 62 percent of the specimens pupated. In this test, 30 percent of the pupae died without producing adults. The effect of temperature on the specimens used in these two tests is more easily demonstrated by observing separately the temperature during the periods of larval development and the temperature during the pupal period.

In the first test, in which all pupae survived, the average temperature during the pupal period was 82.3° F, the maximum was 102° F, and the temperature remained above 100° F for only 7 hours. In the second test, average temperature during the pupal period was 84.6° F. The maximum was again 102° F, but the temperature was at 100° F or above for a total of 32 hours. Here apparently the prolonged exposure was detrimental since 30 percent of the pupae died. It should be noted, too, that in the second test the average temperature of 84.6° F during the period of pupal development was slightly lower than the 84.8° F average for the entire period of development. Thus the increased mortality in the pupal stage indicates that pupae are less resistant to the high temperature than are the larval stages. Specimens were reared as controls at a constant temperature of 70, 85, and 90° F for each of the tests. At 85°

F, 60 to 70 percent of the first-instar larvae produced adult mosquitoes; mortality in the pupal stage was less than 5 percent. At a constant temperature of 70° F adults emerged from over 95 percent of the pupae, but at a constant temperature of 90° F adults emerged from only 60 percent of the pupae.

In other experiments conducted at sustained high temperature, 100 first-instar larvae at 99° F produced 21 pupae, but only one adult; 100 fourth-instar larvae transferred from 85 to 99° F produced 51 adults. The same effect was demonstrated when fourth-instar larvae within a few hours of pupation were exposed to high temperatures. The 24-hour check of mortality would reveal living pupae, but seldom did adults emerge from these same pupae. This delayed effect was not observed when younger larvae were tested; further mortality after the 24-hour check was no greater than that observed in the controls.

Field Studies

Evidence that high temperatures have a detrimental effect on natural *A. quadrimaculatus* larval populations was obtained from field observations. The four-week moving average of the number of fourth-instar *A. quadrimaculatus* larvae taken on routine weekly collections made from Mossy Pond in 1943 varied from zero in January to 19 on May 21. The trends in population fluctuations followed closely variations in the moving average of the maximum air temperatures. In 1943 the average maximum air temperature exceeded 97° F from June 15 to July 7 and from July 29 to September 15. The *A. quadrimaculatus* larval population was decreasing from June 18 to July 9 and from August 7 to September 17.

DISCUSSION AND CONCLUSIONS

Results of tests show that temperatures well within the range of temperatures observed in *A. quadrimaculatus* breeding areas are detrimental to development of larvae. The data shown in Figures 1, 2, and 3 indicate that larval mortality is affected by temperature, time of exposure, and the rapidity with which the temperature changes. Mortality was reduced when the temperature was raised slowly; e.g., in the first series, the indicated 50-percent endpoint for fourth-instar larvae at 107° F is approximately 6 minutes, and for the first-, second-, and third-instar larvae it is approximately 18 minutes, yet in test number 1 of the second series the temperature remained above 107° F for 28 minutes without killing more than 30 percent of any particular instar.

The results show the possible effects of high

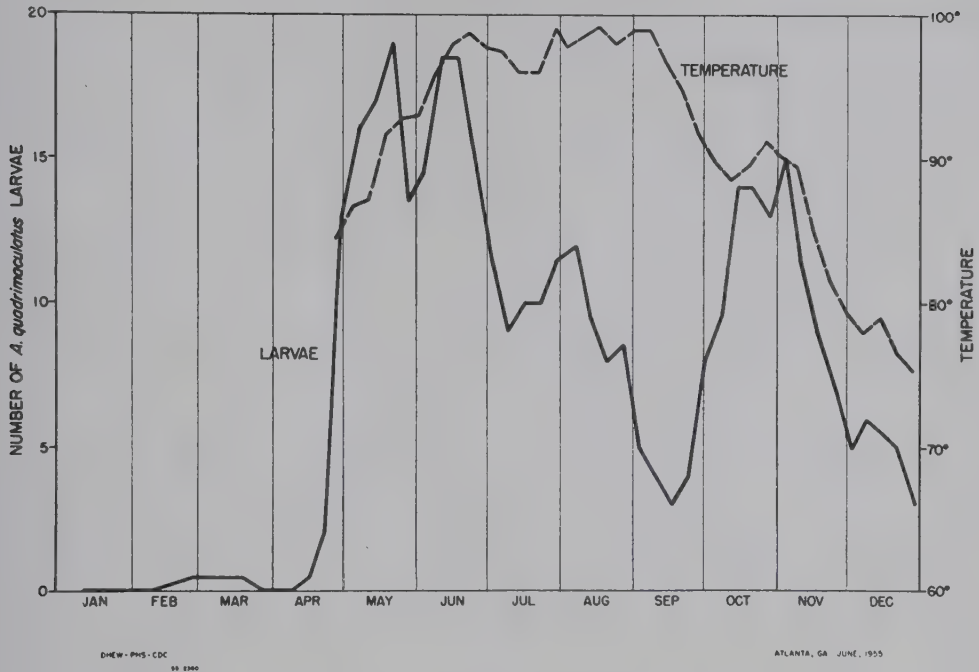


FIG. 4. Relation between four-weeks moving averages of mean daily air temperatures and of number of *Anopheles quadrimaculatus* larvae collected from Mossy Pond, Baker County, Georgia, 1943.

temperatures on *A. quadrimaculatus* larvae in nature. Temperatures a few degrees above 100° F were lethal to 50 percent of larvae, particularly fourth instars, in a relatively short time when temperature changes were rapid. Larvae withstood higher temperatures when the temperature was raised gradually (from 80 to 110° F in approximately 40 minutes). Significant mortality under these conditions did not occur unless the temperature rose to nearly 110° F. This indicates that, in nature, where normally 3 or 4 hours are necessary for the temperature to rise from 80 to 110° F, 50 percent of *A. quadrimaculatus* larvae might survive 110° F or even a few degrees higher.

The ultimate effect of high temperature on pupae is not apparent immediately after exposure. Results of every test indicate that exposure for 2 or 3 hours to temperatures only a few degrees above 100° F greatly reduces the number of adults which emerge.

Field data shown in Figure 4 indicate that an average maximum air temperature of 97° F or above is followed by a receding larval population. At the breeding site from which these data were obtained, a maximum air temperature of 97° F is accompanied by a maximum surface-water temperature of approximately 100-101° F. In

this area daily maxima usually exceed 100° F for air temperature on several days during each summer and may exceed 110° F for surface-water temperature. These data indicate that water temperatures which occur in nature can be detrimental to the development of immature *A. quadrimaculatus*. These detrimental effects probably begin when the water temperature in the breeding area approaches 100° F. Water-surface temperature above 115° F is probably lethal to all aquatic stages of *A. quadrimaculatus*. Since younger larvae can withstand more heat than older larvae and pupae, the length of time necessary for the larval population to recover would be related directly to amount of heat, considering both temperature and time, to which the population was exposed.

SUMMARY

Field observations have indicated that in southwestern Georgia the higher surface-water temperatures which occur naturally in *A. quadrimaculatus* breeding areas are lethal to *A. quadrimaculatus* larvae.

Studies were made to determine quantitatively the lethal effects of high temperatures on *A. quadrimaculatus* larvae and pupae in the labora-

tory and in the field. In some tests, larvae and pupae were subjected abruptly to high temperatures for specific lengths of time and were then returned to room temperature following exposure. In other tests, temperatures were changed slowly. In all tests, fourth-instar larvae were found to be least resistant to high temperatures, followed in order by third, second, and first instars. Pupae were less resistant than larvae. The detrimental effect of high temperature on pupae was not entirely apparent 24 hours after exposure, but was indicated by the failure of viable adults to emerge. All stages could withstand higher temperatures when changes were made gradually. Field observations made during 1943 indicated that in the area studied, average maximum air temperatures above 97° F preceded a decline in populations of *A. quadrimaculatus* larvae. Mortality of immature *A. quadrimaculatus* probably begins as the surface-water temperature approaches 100° F, and is complete when the surface-water temperature approaches 115° F.

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LIFE HISTORY OF *AUSTRALORBIS GLABRATUS*, THE INTERMEDIATE SNAIL HOST OF *SCHISTOSOMA MANSONI* IN PUERTO RICO¹

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INTRODUCTION

In a study of the ecology of *Australorbis glabratus*, the snail intermediate host of *Schistosoma mansoni* in Puerto Rico, in its natural environment, information was sought concerning its life history. Life history phenomena form an integral part of the population ecology of a species; natality, mortality, and dispersion are the factors which determine changes in and survival of a natural population. Of these, both natality and mortality are influenced by the life history of an organism. This is exemplified by the attributes of life history which are: developmental period, reproductive period, post-reproductive period, and fecundity. Any change in these attributes which regulate time of existence and production affect the natality and mortality of the population. Although the effect of different environmental conditions on the life history of *A. glabratus* would be of great interest since they may

directly alter the life history of an organism, this phase of the investigation could not be advanced in the present study. These reported observations on the life history of *A. glabratus* were carried out in the laboratory under more or less optimum environmental conditions to determine growth rate, maximum birth rate, and longevity of *A. glabratus*.

METHODS

Variable conditions in the natural environment of the snail in Puerto Rico made it difficult to conduct such a life history study in the field. Thus a laboratory study was undertaken so that the snails could be maintained under more or less optimum environmental conditions. All studies were conducted in a partially shaded, screened enclosure. Nine hundred snails were individually maintained in glass containers; another 200 snails were kept in pairs in separate containers. Newly emerged snails were maintained until they were 3 mm in size in 20 cc of water containing a small stem of *Najas* sp. All snails 3 mm and larger were reared in 200 cc of water. Each of these aquaria had 1/2 inch of sand on the bottom and

¹ The author is grateful to Dr. C. O. Berg, Mr. K. D. Quarterman and Dr. H. F. Schoof for critically reading the manuscript.

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contained a stem of *Najas* sp. Fresh lettuce, dead leaf, dog food, and yeast were added twice a week. Around the top, on the outside of each glass, a screen or plastic band one inch high was placed to prevent the snails from crawling out.

The water for each aquarium consisted of one-half tap water and one-half stream water. Half of the water was removed from each aquarium weekly and replaced with fresh water. Due to the strong trade winds and heat, evaporation from the aquaria was high. Part of this water loss was replenished by frequent rains. Usually, however, a small amount of distilled water had to be added to each container daily to restore the water level. This procedure prevented the mineral content of the aquaria from increasing excessively.

The temperature of the environment averaged 26.3° C and ranged from 23 to 36 between April 15 and October 15; it averaged 24.7° C and ranged from 21 to 31 degrees between October 15 and April 15.

Snails newly emerged and until they were 5 mm in size were measured with an eye-piece micrometer. Snails over 5 mm in size were measured with a caliper rule. All measurements were for maximum diameter.

To shorten the period of time taken to study the life cycle of this animal which has an expected 2-year life span, the 900 snails used in the study were divided into four size groups. The groups and numbers of specimens contained in each were: newly emerged snails (200); 2.5 to 4.5 mm (300); 9 to 15 mm (200); and 15 to 24 mm (200). All dead snails were noted and replaced with others of similar size so that the growth rate per week could be followed without loss in number. In the analyses of the data, a comparison of mortalities was made between the snails used in initiating the experiment and the snail replacements; no significant difference was noted between the original group and replacement group, so in the final analyses all snails were used.

Mortalities in the four test groups were irregular and averaged about 35 percent for the test period of one year. The highest mortalities occurred when the snails were transferred from stock aquaria to test aquaria. This, however, seemed a natural response of *A. glabratus* to slight changes in the environment (Pimentel and White, in manuscript). Occasionally a heavy growth of algae would develop, especially during cool weather, and kill a few snails. Other snails were undoubtedly killed by handling and measuring.

RESULTS

Egg Stage. The eggs are yellow-brown in

color and oval in shape. The maximum diameter averaged 0.87 mm and ranged from 0.69 to 1.2 mm. They are laid in small masses with each egg surrounded by translucent albuminoid material. Approximately 20 eggs were found in each mass.

A. glabratus has little preference as to placement of its egg masses, for they have been found on the shells of *A. glabratus* and other species, stones, dead leaves, sticks, logs, metal, glass, and on various aquatic plants. A hard surface seems to be the prime requisite.

Emergence of the snail from the egg capsule took an average of 7.9 days and ranged from 6 to 10 days. The percentage of the eggs hatching averaged 72.7 per mass and ranged from 18 to 100 percent. Brumpt (1941) reported the egg stage to be as short as 10 days but usually 15 days at 25° C. This is longer than the results obtained in the present study and those reported by Luttermoser (1943). Brumpt found the percent hatching is 85 and very often reaches 100. The data of this study agree favorably with that of Luttermoser (1943), who found that it took from 8 to 12 days for the eggs to hatch at temperatures between 20 and 29° C and that 64 percent of the eggs hatched.

Young Snail. The newly emerged snail is light yellow in color and translucent. Its maximum diameter averaged 0.731 mm and ranged from 0.52 to 0.95 mm.

The rate of growth was rapid for the young snail until the time of maturity and egg production when growth rate declined (Fig. 1). Growth apparently becomes secondary to egg production once that function begins. The maximum rate of growth occurred when the snail was 1.6 mm in size; at that time the rate of growth for the one following week was 2.3 mm.

Mature Snail. Snails matured and began oviposition at sizes ranging from 6.9 mm to 10.5 mm and averaging 8.41 mm (Fig. 1). These sizes were attained in 7 to 23 weeks, an average of 10 weeks having been required to reach the average maturity size of 8.41 mm. Information reported in the literature is variable. Brumpt's (1941) experimental colonies began laying eggs when the snails reached 10 to 11 mm in size and averaged 8 weeks in age, and ranged between 7 and 9 weeks. The present findings do not agree completely with either Brumpt or Luttermoser. Luttermoser (1943) found oviposition by mature snails occurred when snails attained an average size of 10.0 mm, ranging from 6.0 to 14.0 mm. He states the time to egg production

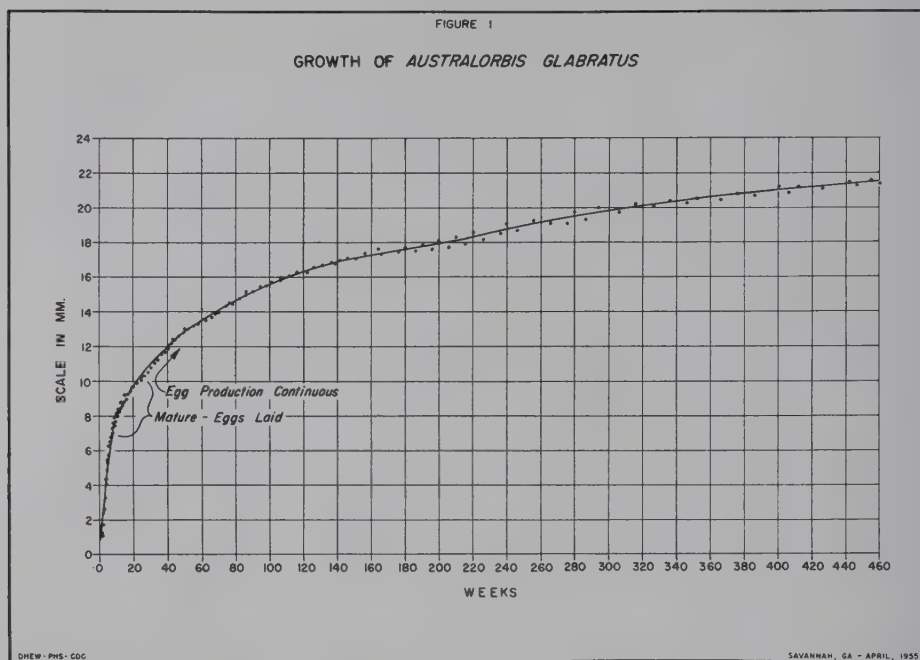


FIG. 1. Growth of *Australorbis glabratus*.

averaged 21 weeks, ranging from 11 to 26 weeks.

A. glabratus are hermaphroditic but they also mate with other individuals of their species. To determine if *A. glabratus* would produce eggs more quickly if allowed the chance to cross-fertilize, 200 snails (2.5 mm to 4.5 mm) were placed in pairs in separate containers. One hundred snails of similar sizes were individually maintained as controls. No difference was detectable in the time to maturity or in the number of produced eggs per snail between the two groups.

The newly matured snails (average size 8.4 mm) produced an average of 1.9 egg masses per week with a range from 0 to 5 masses. The average number of eggs per mass was 10.6 and ranged from 2 to 21. Older snails (average size 19.3 mm) produced an average of 6.8 egg masses per week with a range from 1 to 12 masses. The average number of eggs per mass was 28.1 and ranged from 7 to 51. The older snails produced approximately three times as many egg masses per week with almost three times as many eggs per mass as did the smaller and younger snails. No seasonal effect upon egg production was observed. These data agree favorably with those of Brumpt (1941) who found snails of average size of 24 mm to deposit masses of 80-100 eggs,

while young specimens about 11 mm in size deposit 5-20 eggs per mass. Brumpt also reported no seasonal difference in egg laying.

More eggs were produced by these colonies of *A. glabratus* than by the colonies of Luttermoser (1943). He reported that snails 6 to 19 mm in size produced an average of 15 eggs per week. In this study, snails of an average size of 8.4 mm deposited an average of 20 eggs per week while snails averaging 19.3 mm in size produced 191 eggs per week. The colony of snails studied by Brumpt (1941) produced more heavily than either the colonies in the present study or those in Luttermoser's. In Brumpt's study, snails about 11 mm in size laid approximately 150 eggs per week.

After one year of growth, the snails averaged 13.2 mm in size (Fig. 1). For the same period, Luttermoser (1943) reported an average size of 16.0 mm. Brumpt (1941) found that his snails grew and reached a size of 19 mm in a period of one year. Rapid growth is reported by Chernin *et al.* (1956) who found colonies averaging between 2.3 and 2.5 mm at the outset of an experiment grew to an average size of 12.9 mm in 45 days. The differences between studies are due to the result of differences either in the husbandry,

or genetics, or both of the four experimental colonies.

The largest snail collected in the field by the investigator measured 32 mm. Hoffman and Faust (1934) in Puerto Rico reported the snails "may attain a maximum diameter of 1.25 inches" (31.7 mm). In France, Brumpt (1941) reared snails in the laboratory to a maximum size of 26 mm. Vilardi (personal communication) stated that the largest snail collected in Venezuela measured 35 mm.

DISCUSSION

The present study added more suggestive evidence to the prominent question of the maximum longevity of *A. glabratus*. It is a known fact that *A. glabratus* reaches a maximum size of 35 mm, but the question remains as to how long it would take a snail to grow that large. Investigators' conclusions vary on the postulated maximum longevity of *A. glabratus*: Hoffman and Faust (1934) suggested 1 year; Brumpt (1941) suspected at least 1½ years; Luttermoser (1943) proposed 2 years. Extrapolation from data presented in the growth curve (Fig. 1) indicates it would take about 20 years to reach a size of 35 mm. This seems unlikely, in view of the fact that the colonies of Brumpt (1941) and of Chernin *et al.* (1956) grew at a faster rate than did those of the writer. The effect of the water volume per snail (Baily 1939; Chernin *et al.* 1956) does not explain the differences between the various studies. Brumpt was maintaining his snails individually in 80 cc of water compared to the investigator's 200 cc, and Chernin *et al.* maintained their snails (25 snails per 3-gallon aquarium) in approximately 400 cc of water. Some environmental or genetical factor or factors are responsible for the differences reported, but as yet the factor or factors remain unknown. It is suspected that the maximum longevity of *A. glabratus* is between 2 and 3 years; however, in the natural environment, observations indicate the average longevity to be about 1 year.

The life history described for *A. glabratus* is one of the factors in the ecology of this species which enables it to be one of the most abundant species on the island of Puerto Rico. The snail is not restricted to breeding during a particular season of the year but reproduces all year around. Therefore, whenever environmental pressures controlling the numbers of this species are released it will immediately start increasing its numbers. Fertility is high: one large snail, 19 mm in diameter, can produce about 140 young per week. In addition, with a short pre-reproductive period of

11 weeks, generation cycles are rapid. The maximum birth rate of *A. glabratus* is high.

A. glabratus populations, because they possess a high maximum birth rate, can recover from almost catastrophic environmental situations in a relatively short time. With only a few surviving snails as a start, a stream could be repopulated to near maximum population level in about 3 months. If, for example, a large population of 30,000 snails per 2,700 linear feet of stream (typical of the Quebrada Blasina; Pimentel *et al.* 1957) was flushed from the stream, except for 18 survivors (19 mm in diameter), this would allow the stream to be repopulated. Each snail of this size under optimum environmental conditions producing about 140 young week could repopulate the stream to the original population level of 30,000 individuals in about 3 months. Even taking into account the ecologic pressures of increasing populations in nature, such a stream could still be repopulated within a very few months' time.

SUMMARY

A laboratory study was made of the life history of *A. glabratus*. The egg masses were laid on many types of materials, a hard surface being the prime requisite. Each mass contained approximately 20 eggs which averaged 0.87 mm in size and hatched in an average of 7.9 days. An average of 72.7 percent of the eggs hatched.

The newly emerged snail averaged 0.731 mm in diameter. Oviposition began when the snail averaged 8.41 mm and was 10 weeks of age. Egg production was continuous after maturity without seasonal variation. The large snails (19.3 mm) produced more eggs than smaller snails (8.41 mm). Rate of growth was slower after egg production began.

The maximum birth rate of the species was high, the egg-to-egg period requiring only 11 weeks. A large mature snail may produce approximately 10,000 eggs per year.

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FURTHER NOTES ON THE POPULATION ECOLOGY OF THE SPADEFOOT TOAD

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The purpose of this paper is to supplement and in some cases revise the information on the population ecology of the spadefoot toad (*Scaphiopus h. holbrookii*). In an earlier paper by Pearson (1955), studies on three adult, terrestrial populations were described. One of them was a natural population located in a study area (plot 1) that included a grass prairie, a hardwood forest, and the ecotone between them. The plot measured 200 x 300 feet. A 100-ft grid system was surveyed first and later three areas were surveyed in a 10-ft grid system. The intersection of grid lines was marked by stakes and the lines were numbered and lettered. This plot was intensively studied from July 19, 1951, to August 27, 1953. The toads were easily caught during their nocturnal emergences from burrows, they were marked by a toe clipping method, measured with vernier calipers, and then they were released for future recapture. Data collected in this manner led to conclusions concerning their activity rate and the factors affecting it, their spatial distribution, home range, territoriality, densities and density effects, survival and disappearance rates, and individual growth rates, as presented in the earlier paper.

Additional data are now available as a result of studies on this natural population by Dr. Richard L. Highton on July 6 and 17 and September 11 and 22, 1954, and by the more extensive work of Mr. J. Alan Holman on October 8, 10, 29, November 9, 10, December 2, 5, 1955, and February 3, April 16, 23, 1956. The author made observations on June 13, 29, 30, 1956. I am deeply grateful to these gentlemen for their help in this work that has extended the observation of a spadefoot population under field conditions to nearly five years.

SPECIAL RELATIONS

Detailed descriptions of spadefoot home ranges along with an analysis of factors influencing home range size were given by Pearson (1955). Homing behavior over extended round-trips as great as $\frac{1}{4}$ mile was recorded and many observations of behavior relative to movements around the burrow in the home range led to the general conclusion that the toads were spatially well-oriented. The duration of recorded use of a home range lasted the full course of the 1951-53 study for many of the toads studied.

It was indeed interesting, then, to find that some of the toads originally seen in July, 1951, had remained in the same home range until 1956. For example, female #104_s was retaken June 29, 1956, well within the range of capture sites recorded between 1951 and 1953 (Fig. 1). At this time of capture the toad was within two feet of its burrow into which it retreated. This burrow was known to have been in use since March 12, 1952, or for a period of over 51 months. It can be seen in Figure 1 that #415 remained within the area of its small range, #331 had moved about 143 feet, #104 was less than 13 feet from its old burrow and #1033 was within its old capture range. The records of duration of home range maintenance are longest in the case of #104_s (59 + months), #415 (58 months), #331 (57 months), #104 (55 months) and #1033 (50 months). Of the 20 animals recaptured in 1954-56 whose range was well known in the earlier study, 15 were within 20 feet of previous burrows or home range centers. Only one of the 20 toads had moved more than 100 feet.

Another measure of spatial stability is shown in the records of maximum distance between points of capture. Data on movements of 395 individuals

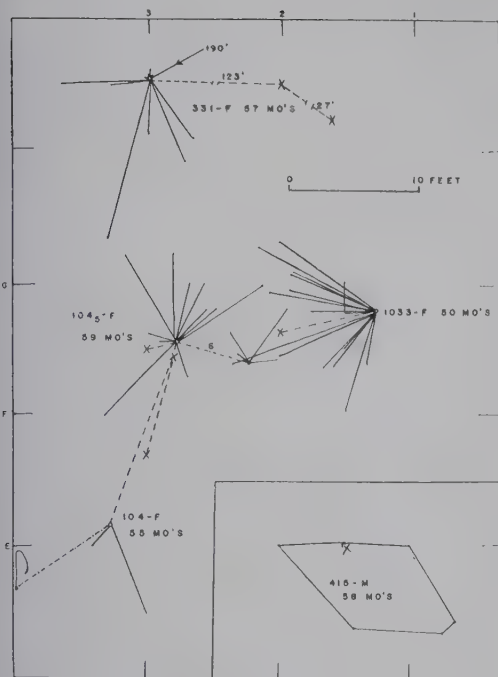


FIG. 1. Home ranges of individuals retaken during the study. O = burrow; — connects capture point with burrow assumed to be in use; - - - movement of burrow site; number over latter indicates times burrow use alternated; x is capture site during recent study; --- connects recent capture with burrow last in use. The number of months indicates length of time the home range was under observation.

TABLE I. Frequency of greatest distances between capture sites for toads recaptured during the 1954-56 studies

Feet	1-26	Months of observation 36-48	49-59
1.....	2	..	..
4.....	..	1	..
7.....	..	..	..
10.....	1	2	..
13.....	3	..	1
16.....	5	2	2
19.....	4	2	1
22.....	..	..	1
25.....	2	..	..
28.....	..	2	..
31.....	2	..	1
34.....	..	..	..
37.....	..	..	..
40.....	2	..	..
43.....	1	1	..
46+.....	4 (52, 61, 70, 175)	9 (55, 58, 61, 82, 101, 113, 115, 130, 153)	6 (49, 58, 71, 100, 150, 193)

for the duration of the 1951-53 study indicated that the great majority did not move more than 32 feet and that only a few moved more than 107 feet (Pearson 1955). The 1954-56 recaptures of toads marked in the original study were used to calculate dispersal distances and these are given in Table I. Again, it is seen that the majority was recaptured less than 32 feet from any other capture site and even after between four and five years of observation six of 12 toads were recorded within 32 feet maximum distance moved.

On the other hand it should be noted that since observation was concentrated in a small plot, the probability of capturing toads at long dispersal distances was not as great as for short distances. However, in the earlier study attempts were made to observe marked toads that had dispersed out of the plot but none was found beyond the immediate boundary of the area, except during breeding migrations. During the 1954-56 studies no efforts were made to find marked toads at great distances outside the plot.

SURVIVAL AND DISAPPEARANCE

A study of survival and disappearance rates was based on a cohort of 153 individuals that were first observed between July and September, 1951. This group provided individuals that had been observed for the longest period. The time interval used in these studies is three months for the records through June, 1953, while for those data taken later the time unit is variable since either a full three months were not studied or insufficient data were collected in this period. Survival was calculated on the basis of the percentage of the original 153 individuals that was known to be alive at the beginning of the particular time interval. These percentage values could also be expressed as the number surviving at the beginning of the time interval out of an original 100 toads.

The rate of loss or disappearance was calculated as the number lost during the time interval divided by the number surviving at the beginning of the time period, and it is expressed as a rate per 100 toads per three months. The disappearance rates are made up of "apparent" loss from lack of observation, of loss from death, and of loss due to dispersal from the study area.

Additional work of the last three years has led to a revision of the survival and disappearance rates given in the earlier paper (Table II). For each of the time periods the survival percentage has been increased and the loss rate values have been decreased. This decrease from the rates of loss

published earlier by Pearson (1955) results from at least a partial elimination of the "apparent" loss component. In other words, the recent studies have recorded the presence of individuals in the study plot that were not observed during the later months of the 1951-53 period and thus were recorded as lost. It should be stressed that the values given for the 1954-56 period might be changed in a similar way if additional observation could be made in the near future.

TABLE II. Survival and disappearance rates for a selected cohort of 153 spadefoot toads. A time interval of 3 months is used through June, 1953, and one of variable length thereafter

Date	PEARSON (1955)		REVISED CALCULATIONS	
	Per cent surviving at start of period	Loss rate per 100 alive at start of period	Per cent surviving at start of period	Loss rate per 100 alive at start of period
1951				
Oct. through Dec.....	79.7	25.4*	86	19.6
1952				
Jan. through Mar.....	71.2	10.7	72.5	9.8
Apr. through June.....	67.3	5.5	69.3	4.5
July through Sept.....	62.8	6.8	64.7	6.6
Oct. through Dec.....	58.8	6.3	61.4	5.1
1953				
Jan. through Mar.....	55.6	5.6	58.2	5.3
Average.....		10.0*		8.5
1953				
Apr. through June.....	40.5	27.1	43.8	24.7
July through Aug.....	27.5	32.3	30.7	29.9
1954				
July through Sept.....			10.4	68.1
1955				
Oct. through Nov.....			5.9	40.0
1956				
Feb. through June.....			2.6	55.5

*Due to arithmetical errors, the rate of loss for the period October through December, 1951, was incorrect as published. The value should be 20.3 and the average through March, 1953, should be 9.5

Concerning disappearance of toads attributed to dispersal from the area, it was shown in the 1951-53 study that an association existed between rainfall and toad dispersal as measured by the rate of immigration of new toads. The greatest immigration was recorded during and immediately after the four breeding periods on September 17, 1951, February 15, 1952, April 7, 1953, and August 23, 1953. At the same time, increased disappearance rates were noted during the time intervals that included the reproductive dates listed above. Therefore we have evidence of increased population shifts during breeding periods through measurements of immigration into the population, as well as through disappearance of toads from the cohort of 153 used for survival studies.

With additional data from the recent studies

the average rate of loss was revised to 8.5 toads per hundred per three months for the period from October, 1951, through March, 1953. If it were true that a large part of the disappearance recorded in this time period was associated with dispersal during reproductive choruses, then a closer approximation to actual death rate would be found for the period April, 1952, through March, 1953, during which no breeding occurred. The average rate of loss for this period was 5.37 toads per 100 per three months.

In addition to the survival data shown in Table II it should be noted that three (2.0 percent) of the original 153 toads were known to be alive in April, 1956, and one (0.7 percent) was alive in June, 1956.

In the preceding discussion, the fate of 153 individuals served as the base for calculations. Another approach to the study of survival and rate of disappearance is the turnover of the population that was marked prior to the breeding on August, 23, 1953. Capture data for four field trips during late August, 1953, are given in Table III; they show the effect of the breeding dispersals on the reduction of the percentage of marked toads in the population. This effect is illustrated by the fact that retake percentage was 100 on August 18, the same as on many earlier trips, while it fell to 89 percent when the rain began on the 22nd and to 64 and then 54 percent during and after the breeding. Therefore, if the sample data for August 27 accurately represent the population, only 54 percent was marked and observed as a part of the pre-breeding population.

TABLE III. Capture and recapture data pertinent to the 1954-56 study. Figures in parentheses give the percentage of total capture comprised by animals previously marked

Date	Total captures	Number Pearson retakes (%)	Number Highton marked	Number Highton retakes	Number Holman marked	Number Holman retakes
1953						
August 18.....	26	26 (100)	..		..	
August 22.....	27	24 (89)	..		..	
August 24.....	28	18 (64)	..		..	
August 27.....	28	15 (54)	..		..	
1954						
July - Sept.....	27	11 (41)	16		..	
1955						
Oct. - Feb. '56..	72	20+27 (28)	..	2 (3)	48	
1956						
April.....	27	5 (19)	..	2 (7)	12	8 (30)
June.....	24	4 (17)	..	2 (8)	11	7 (29)

The 1954-56 capture data are also given in Table III. They show that the population marked prior to August 23, 1953, is represented by a decreasing percentage of the total captures in

these later periods. This proportion of toads marked in the earlier study to the total population sampled in the 1954-56 study was reduced 13 percent in 10½ months to July, 1954; 13 percent the next 15 months to October, 1955; 9 percent the next 6 months to April, 1956; and two percent the next two months to June, 1956, for an average decrease of 1.09 percent per month or about 13.08 percent annually.

POPULATION DENSITY

In the 1951-53 study, several population census techniques were used. It was found that a simple count of the population gave inaccurate results since only a small part of the total population was active at any one time. Another method, the adjusted count, was a count of toads per census period that was adjusted by adding to this simple count the toads that were observed *both* before and after the census period under consideration. For example, to the simple count of individuals observed in the census period of July, 1953, would be added an individual that was observed in June and August, 1953, but not in July. Thus, it is assumed that the animal was present, but unobserved, during the time interval. This technique underestimates the population at the beginning and the end of the study, as a result of failure to observe the animal preceding the early observation periods and subsequent to the later ones.

The capture of toads during the 1954-56 study that had been marked during the earlier study provided data for revision of the adjusted count results published by Pearson (1955). The adjusted counts for the ecotone from the earlier study and the revisions of these counts allowed by the new data are given in Table IV. The

TABLE IV. Population estimates for a prairie-forest ecotone. See text for discussion of the methods used in the adjusted counts and Hayne modified ratio estimates

Date	ADJUSTED COUNTS			Estimated by Hayne modified ratio
	Pearson (1955)	Revised by 1954-56 study	No. per acre	
July, 1951-Sept., 1951.....	97	97	546.8	192.2
Oct., 1951-Jan., 1952.....	132	133	626.3	187.9
Mar., 1952-May, 1952.....	127	129	607.5	178.2
June, 1952-Aug., 1952.....	120	123	579.2	84.4
Sept., 1952-Dec., 1952.....	130	133	626.3	148.4
Jan., 1953-Mar., 1953.....	130	134	631.0	129.5
April, 1953-June 6, 1953.....	97	103	485.0	93.4
June 13, 1953-June 30, 1953...	92	100	470.9	85.4
July, 1953.....	47	55	259.0	49.7
August, 1953.....	78	86	405.0	58.4
July, 1954-Sept., 1954.....	...	37	174.2	121.0
Oct., 1955-Nov., 1955.....	...	52	244.9	241.0
Dec., 1955-Apr., 1956.....	...	39	183.7	121.0
June, 1956.....	...	27	127.0	

greatest revisions in the counts are for the last census periods of 1953. These are intervals for which there had been no follow-up observations. Adjusted counts are given in Table IV for the 1954-56 periods but it is again emphasized that they underestimate the population since (1) the toads could have been present but remained inactive and unobserved and (2) there were no later observations in the area to record these individuals as they became active. The number of toads per acre of ecotone habitat was calculated using the adjusted counts revised by this 1954-56 study.

Another census technique that was used employs the modified ratio method that was discussed by Hayne (1949). Using capture records of marked and released individuals this modified ratio is based on the idea that the percentage of retakes for any particular field observation varies linearly with the number of animals previously marked and released. To obtain the population estimate one must find the trend line that passes through the origin on the *X* and *Y* axes and best fits the data; the population size can be calculated directly with the following formula:

$$P = \Sigma \frac{W X^2}{W X Y}$$

where *W* is the number of captures per field trip, *X* is the number of animals previously marked and released, *Y* is the proportion of the catch that had been previously marked, the summation is for data from each of the field trips in the census period, and *P* is the population estimate. For a more detailed discussion of this method and for assumptions involved see Hayne (1949).

From Table IV a comparison of population estimates made by the adjusted count and by Hayne's modified ratio method is possible. Since the adjusted count underestimates the population at the beginning and the end of the study, the best estimates from this technique would probably be from March, 1952, through March, 1953. The estimates of population size by the Hayne method are taken from the earlier study, except for the 1954-56 periods. The difference between number estimated by the modified ratio in relation to the revised adjusted counts is + 49.2 for March through May, 1952; - 39 for June through August, 1952; + 15.4 for September through December, 1952; and - 4.5 for January through March, 1953. A Chi-square analysis of the frequencies of the adjusted count and ratio method estimates from March, 1952 through March, 1953, gives evidence that they could be as different as

observed due to chance factors alone in less than one time in a hundred ($\chi^2 = 33$, $P < 0.01$). Therefore, it is concluded that there is a significant difference between the population estimates from the two methods. The greatest contribution to the Chi-square value was for the March through May and the June through August, 1952 periods.

GROWTH

Observed long-range growth data given in Figure 2 are to be compared with statistically calculated average growth rates that were given by Pearson (1955). The observed growth of head width for five individuals whose age was known or could be closely estimated and for which long-range data were available is given. Note that the growth curves for the two females (3005 and 2134) closely follow the calculated growth curve.

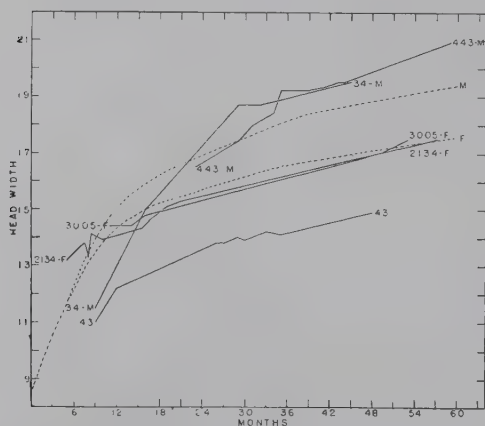


FIG. 2. Head width growth data expressed in millimeters. Dotted lines represent calculated average growth while solid lines are observed growth.

The two curves for males (443 and 34) indicate a difference in rate of growth from the average and point up the fact that the calculated curve represents the average and thus departures from it are to be expected.

Of interest is the growth of #43 that was significantly behind that of normal toads. This toad had not developed any sexual characteristics observable without dissection even though the average male and female attain them at 15 and 19 months respectively (Pearson 1955).

DISCUSSION

Observational data on spadefoot toad home ranges over long periods of time indicate considerable spatial stability. Toads observed for between four and five years remained in very

small and localized areas. Data on maximum distances between capture sites for toads observed for up to five years also indicate relatively short dispersal distances. Similar spatial stability has been reported for the salamander *Ensatina eschscholtzi xantopica* by Stebbins (1954) and for *Batrachoseps attenuatus* by Hendrickson (1954), but apparently this degree of stability has not been reported for an anuran. It would seem to depend on a homing reaction and a well-developed ability to orient within the home area such as was reported by Pearson (1955).

Survival of spadefoot toads was observed for nearly five years on a beginning cohort of 153. Rates of loss per unit time were also calculated from these data and it was pointed out that the loss was (1) an "apparent" loss due to lack of observation of toads that were actually present, (2) loss due to dispersal from the study area, and (3) loss due to death. An evaluation of the relative importance of these components is desirable.

The "apparent" loss is probably quite low for the 1951-52 periods since considerable study in the plot in 1953 gave ample opportunity to observe individuals if they were present. The 1953 data as published by Pearson (1955) contained a considerable component of "apparent" loss, but this has been largely eliminated by the addition of new data in the 1954-56 studies. It is therefore felt that the "apparent" loss for the 1951-1953 period is small. However, it is probable that this component of loss is a sizeable factor in the rates of loss for the 1954-56 study periods.

The loss-by-death item would seem to be small since the density changed very little through March, 1953, and since reproduction of young during this period was very small (Pearson 1955). The obvious conclusion that the greater disappearance rates during the breeding periods result in the main from loss by dispersal to adjacent areas is clouded by the fact that none of these marked toads was observed in nearby areas. Therefore, the relative contribution by death and by dispersal cannot be evaluated in this study.

An evaluation of the survival values obtained during the 1954-56 study for the cohort of 153 toads is needed. Since the number of toads being observed for survival was small and since only a small part of the total toad population may be active at one time, it is most probable that the observed survival values are too low and would have been higher if more observations of the population had been made.

For comparison with these observed survival values we could estimate survival if we assume

that the average rate of loss for the 1954-56 period would be 8.5 toads per 100 per three months, as it was during the earlier study. If we begin with the 47 toads (of the original 153) known alive in July, 1953, at this rate of loss we might expect survival of 20.2 percent in July, 1954; 13 percent in October, 1955, 11 percent in April, 1956, and 10.3 percent in June, 1956. The first of these values is double and the last is ten times greater than the observed survival. The true survival is probably somewhere between the observed and this extrapolated value.

With knowledge of the density changes, survival could also be estimated using the population turnover values that were based on the total marked population. For example, if we assume the density did not change in order of magnitude, we could expect that losses due to death and dispersal would be compensated by immigration, and that the decreases in percentage of retakes for animals marked in the earlier study would estimate rate of loss. Therefore if, for example, we multiply the 47 individuals known to survive in July, 1953, by the percentage of the population retaken in July, 1954 (41 percent), we would arrive at an estimated survival of 19.3 toads (12.6 percent). Likewise, we could calculate survival of 13.2 toads (8.7 percent) for October, 1955, 8.9 toads (5.8 percent) for April, 1956, and 8 toads (5.3 percent) for June, 1956. Again, these figures are greater than the observed survival values.

However, whether one uses the lower observed survival or either of the two higher extrapolated values, the general conclusion is that the spadefoot toads in this study have much greater longevity and a much lower population turnover than previously reported for an anuran. Blair (1953) in a study of juvenile Mexican toads (*Bufo valliceps*) estimated that about 11 percent of the marked males survived to sexual maturity. Jameson (1955) has concluded that the cliff frog (*Syrrophus marnocki*) has a complete turnover of its population within three years. He also reported losses as high as 45.3 percent of this population during the spring of 1950 and 54.0 percent during the fall of 1951. In no season were losses of spadefoot toads at this level of magnitude. Jameson (1956) has also reported very high population turnover in a *Hyla regilla* population.

As a result of additional data collected in the 1954-56 study, the adjusted counts of individuals in the ecotone habitat from July, 1951, through August, 1953, were revised and considerable reliability is attached to these counts from March, 1952, through March, 1953. However, these

counts of the population are considerably different from those estimated by the modified ratio method of Hayne (1949). The greatest differences are for the March through May, 1952, period where the ratio method was considerably higher, and for the June through August, 1952, period where this ratio method estimate was considerably lower. The factors that might cause divergence for the first period are unknown. However, for the summer period where the ratio method underestimated the population in relation to the count, a possible explanation was given by Pearson (1955).

The population estimates obtained by the modified ratio method of Hayne (1949) for the 1954-56 study are not based on as large samples nor are these samples as conveniently spaced over relatively short periods of time as were those in the original study. Therefore the likelihood of error is greater for these estimates. It is the author's judgment that the value of 241 for the period from December, 1955, through April, 1956, is too high.

Concerning the comparison of observed growth of head width with that of calculated average growth, considerably more data are needed to make a satisfactory judgment of the reliability and usefulness of the calculated curve. The records that are given are for general comparative purposes.

SUMMARY

1. Spadefoot toads have been recorded in the same home range area for as long as 59 1/2 months while many of the animals were apparently using the same range for four years or more. One individual was recorded from the same burrow for a period of 51 months. All data lead to the conclusion that the spadefoot has considerable spatial stability and is well oriented within its range.

2. After nearly five years of study, half of the greatest recorded distances between capture sites is less than 32 feet. These data again lead to the conclusion that this species maintains rather limited home areas.

3. Survival and disappearance rates based on a cohort of 153 toads first recorded from July through September, 1951, have been revised as a result of data collected through June, 1956. The rate of loss for the period from October, 1951, through March, 1953, averaged 8.5 toads per 100 per three months.

4. Some estimates of population turnover were made that were based on decreases in the proportion of toads marked and released prior to August

23, 1953, in the collections during 1954-56. These data were used as another estimate of survival.

5. Revision of the measurements of density was also made possible by the field work of 1954-56. The adjusted counts were revised and then compared with estimates made by the modified index method.

6. Some long-range records of the growth of greatest head width are compared with average growth curves predicted statistically; however, additional observed data are needed before an evaluation of the average curve can be made.

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DETERMINATION AND ANALYSIS OF RECURRENT GROUPS

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INTRODUCTION

The primary information available from an ecological survey usually consists of a mass of sampling results involving many localities and many species. In order to investigate the interspecific processes which may be involved in controlling the abundance and distribution of the species found, it is useful to be able to group together those species which frequently occurred together in the samples, which were in this sense a nearly constant part of each other's biological environment. The grouping will be most valuable as a classificatory device if it consists of defined units obtained by a procedure which can be repeated. Whatever the method of grouping employed, the sampling procedure is certain to introduce subjective elements; the size of sample, the number and selection of sampling sites and the sampling methods used will always be influenced by the judgment of the person doing the study and they will in turn influence the composition of the groups. If, however, the sampling conditions are explicitly given, the probable extent and character of these influences can be taken into account and a meaning given to the groupings in this context.

Some of the methods of grouping which have been suggested will be briefly reviewed (see also Macfadyen, 1954) and a new method will be outlined which overcomes some of the difficulties

found in the others. This method of grouping uses the concept of affinity in the sense suggested by DuRietz (1932); those species which rather often form mixed populations have a strong affinity, those which never do so have no affinity. A new index is proposed which defines the words "rather often" in the preceding statement. With this as a basis, a procedure has been developed which leads to the largest, most frequent, separate units within which each species shows a strong affinity with all others. It may be expected to be most useful when applied to studies of animals which are difficult to observe directly and which must, therefore, be studied initially by sampling procedures.

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REVIEW OF SOME METHODS OF GROUPING

Animals have often been grouped on the basis of vegetation or of various physical or chemical factors in the environment, but many difficulties are involved in vegetational classification or in deciding what is a critical limit in respect to a certain physical or chemical factor. Furthermore, animal groupings do not always conform to vegetation or other factors; a group may extend over several recognizable vegetation or soil divisions or there may be several distinct assemblages of animal species within an environmental complex which is uniform in many other respects. The characterization of the habitat in which an animal group is often found must include the associated plants and other factors, but it seems better to use the animals as the primary basis for their grouping.

Gisin (1947, 1949, 1951) has suggested a procedure using what he has called "differential" species. In the hands of an experienced worker this method can lead to useful groupings, but the choice of the species which will be designated as "differential" is so subjective that comparison between groupings by different workers, even if based on the same material, may be impossible. Moreover, using this method groups may be suggested the constituent species of which so seldom occur together that it seems unlikely that they could have any relation to each other. For example, Gisin (1947) in his rearrangement of Agrell's (1941) Swedish Lapland Collembola suggested four groups. Members of three of these were found together moderately often. The fourth group contained four species, representatives of which were recorded in a total of thirty-one samples; no sample contained all four, one sample contained three, five samples contained different pairs and twenty-five samples contained only one of the species.

The subjective element can be reduced if the grouping is based on a defined index of affinity. Perhaps the simplest expressions which might be used for this purpose are those proposed by Jaccard (1908) and Sørensen (1948) as measures of the similarity between floras. As given, however, neither differentiates between a coefficient based on ten samples and one based on one thousand samples, though the latter would surely be a more reliable estimate. The expressions also fail to take account of changes in the relative number of total occurrences of the two species; as long as the sum of the total occurrences remains constant, the proportions can change without affecting the value of the coefficient.

A method based on correlation between pairs of

species is precisely definable but, as Cole (1949) has pointed out, product moment correlation cannot be used directly because sampling results for most species are not normally distributed in regard to numbers of individuals per sample; there are usually a few outsize samples which will have a disproportionate effect on the calculations. Transformation of the data or the use of rank correlation could overcome this difficulty, but any method which involves a measure of abundance may, in certain cases, not lead to the desired results: two species may always occur together and never separately and yet, unless there is a nearly constant relation between the relative numbers of individuals of the two species, a correlation coefficient will indicate no relationship even though they are a constant part of each other's biological environment. For this reason it seems best to base species groupings upon presence and absence alone and to consider abundance relations within such groupings after they have been determined.

In his paper, Cole (1949) discussed the coefficients of association which had been proposed up to that time and indicated the deficiencies of each. He then proposed a new coefficient using only presence and absence and based on a 2×2 contingency table for which a Chi-square test of significance can be calculated. A basic assumption of his expression is that all samples taken should be included; *i.e.*, the probabilities of occurrence of the two species being tested for association are assumed to be uniform throughout the area sampled. Under this assumption, the Chi-square indicates the significance of the departure of the observed number of joint occurrences from the number expected on the hypothesis of independent distribution of the two species over all the samples. Although Cole did not use his coefficient for grouping species, it has been so used several times since. The following example shows that it is not a satisfactory criterion for grouping if the groups are to be composed of species which form a nearly constant part of each other's biological environment:

Species (1)		
Species (2)	Present	Absent
Present	50	10
Absent	10	2
$\chi^2 = 0.00, p \sim 1.0$		

Species (3)		
Species (4)	Present	Absent
Present	5	8
Absent	8	51
$\chi^2 = 4.46, p < .05$		

Species 1 and 2 show no evidence of association when examined by Cole's method and yet they nearly always occur together—over 80% of the occurrences of each are in company with the other—and should be considered together in any grouping based on this set of samples. On the other hand, species 3 and 4 are significantly associated by Cole's criterion even though their affinity is rather low—less than 40% of the occurrences of each are in company with the other. In general, two species which occur in most of the samples taken will show little or no evidence of association and two species with a low percentage of joint occurrences can show significant evidence of association if they are rare enough or if a large enough number of samples in which they could not occur are included. Bray (1956) has recently noted these difficulties connected with the use of Cole's index and has attempted to overcome them by considering only quadrats within plots in which both species occurred. Macan (1954) using the method without modification found a very large number of positive associations in his analysis of collections of Corixidae, a finding which, as he indicated, was unsatisfactory because the objective analysis produced a less well-defined picture than that which could be obtained from a subjective technique based on a knowledge of habitat features.

INDEX OF AFFINITY

An expression of the sort suggested by Cole has certain desirable properties; in particular, it is sensitive to changes in the relative frequency of occurrence of the two species and a "significance

$$t = \left[\frac{(n_A + n_B)(2J - 1)}{2n_A n_B} - 1 \right] [\sqrt{n_A + n_B - 1}].$$

A *t*-test is preferred to Chi square because it can be used as a one-tailed test [$1.645 \sim p(.05)$] for positive affinity; negative affinity, being based on the failure to find a species, seems potentially subject to too many unavoidable errors.

There are both mathematical and biological reasons for setting an upper limit on the value of n_B which will be considered with a given n_A : the closer the ratio n_B/n_A is to 1, the closer the normal approximation will be to the true value; keeping the ratio close to 1 ensures that whenever evidence of affinity is obtained the number of joint occurrences will be a considerable proportion of the total number of occurrences of both of the species. This is a desirable property for an index to be used as a basis for grouping if the purpose is to put together organisms which are a nearly constant part of each other's biological environment. An upper limit of 2 for the ratio n_B/n_A is therefore sug-

gested. The use of such a limit has the disadvantage of preventing the finding of affinity between such a pair of species as a rare parasite and its relatively abundant host, but the existence of a relationship of this kind can, in any case, probably be satisfactorily established only by field observation and breeding studies.

level" can be defined for use as an objective criterion of the presence of affinity. It can be adapted for use as an index of affinity if it is assumed that the probability of finding species A is $n_A/n_A + n_B$ and of finding species B is $n_B/n_A + n_B$, where n_A is the total number of occurrences of species A and n_B is the total number of occurrences of species B; i.e., the probabilities of occurrence of the two species are related to the sum of their occurrences ($n_A + n_B$) rather than to the total number of samples taken. The use of this assumption removes the premium on rarity and also makes it possible to find evidence of affinity between two species which occur in most of the samples taken. It seems neither more nor less arbitrary than the use of the total number of samples for the latter is usually determined arbitrarily by the person doing the work, often mainly on grounds of practicality or subjective judgment that the number taken is sufficient.

If the preceding assumption is used and the species are assigned to the letters so that n_A is less than or equal to n_B , the number of joint occurrences (J), on the hypothesis of independent distribution, will have a hypergeometric distribution with expected J equal to $n_A n_B / (n_A + n_B)$ and variance equal to $(n_A n_B)^2 / (n_A + n_B)^2 (n_A + n_B - 1)$. For values of n_A greater than 10 and p and q not too different from $1/2$, a normal approximation can be used to test the significance of the deviation of the observed number of joint occurrences from the expected number. For this purpose, the following expression can be taken as a normal deviate with mean 0 and unit variance (Pearson 1947):

gested. The use of such a limit has the disadvantage of preventing the finding of affinity between such a pair of species as a rare parasite and its relatively abundant host, but the existence of a relationship of this kind can, in any case, probably be satisfactorily established only by field observation and breeding studies.

Minimum values of J which are significant at the .05 level have been calculated for values of n_A from 5 to 10 using exact probabilities obtained by Leslie's method (1955). Similar values have been calculated for each tenth value of n_A from 20 to 100 using the normal approximation. Both sets are given in Table 1 in the Appendix. These values and intermediate ones which can be estimated by interpolation will make it possible to quickly sort pairs of species into those which certainly show evidence of affinity, those which cer-

tainly do not and those which are doubtful and require calculation.

When applied to the examples used in the discussion of Cole's coefficient, the index proposed above indicated significant evidence of affinity between species 1 and 2 but none between species 3 and 4. It is, therefore, a better index of the proportion of occurrences which are joint occurrences and should provide a more satisfactory basis for grouping. It may be repeated that Cole did not develop his index as a basis for grouping and that the two indices measure different things: Cole's index measures the departure of the two species from independence of distribution on the assumption that the probability of occurrence of each is constant over all the samples taken; the index proposed in this paper provides an objective measure for the word "frequently" in the statement "these species frequently occurred together."

DETERMINATION OF RECURRENT GROUPS

The procedure to be outlined for the determination of recurrent groups may appear complicated but with a little practice it can be gone through at least as rapidly as the "fitting by eye" of a trellis diagram. It has the virtue of repeatability; given the same primary information, two workers will always arrive at the same groups. This means that if several workers using similar sampling methods make studies in different localities and find different recurrent groups, there is some assurance that the differences are real and not the result of differences in judgment or emphasis. Any dichotomous index of relationship between species can be used as a basis for grouping by this procedure; the meaning of the groups will be determined by the nature of the attributes measured by the index.

In this paper, a recurrent group is defined as one which satisfies the following requirements:

- (1) The evidence for affinity is significant at the .05 level for all pairs of species within the group.
- (2) The group includes the greatest possible number of species.
- (3) If several groups with the same number of members are possible, those are selected which will give the greatest number of groups without members in common.
- (4) If two or more groups with the same number of species and with members in common are possible, the one which occurs as a unit in the greater number of samples is chosen.

These requirements are to be taken in order; *i.e.*, the group or groups which fulfill requirements 1

and 2 are determined and then, if there are several possible combinations, a choice is made on the basis of 3, followed, if necessary, by 4. Such groups will represent the largest, most frequent, separate units within which all the species formed a nearly constant part of each other's biological environment. They would be a likely choice if one wished to make an intensive study of interspecific processes which are quantitatively important in the habitats sampled.

The following procedure will give a recurrent group or groups as defined above. The affinity information for the species concerned may be set out in a trellis diagram as shown for the example (Table I). If there are many species, it has been found more convenient to record the information for each species on a separate card.

TABLE I. Affinity between pairs of species

	SPECIES															Number of affinities
	A	B	C	D	E	F	G	H	J	K	L	M	N	P	Q	
A	+	+	+	+	+	+	+	+	+	+	+	+	.	.	+	12
B	+		+	+	+	+	+	+	+	+	+	+	.	.	+	9
C	+	+		+	+	+	+	+	+	+	+	+	.	.	+	9
D	+	+	+		+	+	+	+	+	+	+	+	.	.	+	9
E	+	+	+	+		.	+	+	+	+	+	+	+	.	+	8
F	+	+	+	.	.		+	+	+	+	+	+	+	+	+	7
G	+	+	+	+	+	.		.	.	.	.	+	+	+	+	7
H	+	+	+	+	.	.	.		.	.	.	.	+	+	+	6
J	+	+	+	+	.	.	.	.		.	.	.	.	.	.	5
K	+	+	+	+	+	.	.	.	.		.	.	.	+	.	5
L	+	+	+	+	+	.	.	.	.	.		.	.	.	.	4
M	+	.	.	+	.	.	.	.	.	.	.		+	.	.	4
N	.	.	.	.	+	+	+	+	.	.	.	+		.	.	4
P	.	.	.	.	+	+	+	+	+	+	.	.	.		.	4
Q	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	3

+ = affinity; . = non-affinity

The species are put in order in terms of the number of other species with which they have affinity. In the example this order is A, B, C, . . . P, Q. Starting with the species with the largest number of affinities, species are counted in the direction of decreasing number of affinities until the number of species counted (X) exceeds the number of affinities (Y) of the last species counted. In the example this occurs at species H where $X = 8$ and $Y = 6$.

Two possible relationships between X and Y must now be considered:

[$X \leq Y + 2$] If this is true, as it is in the example, the largest potential group will contain $Y + 1$ species; 7 species in the example. It cannot contain more because species H has affinities with only 6 other species and can, therefore, only form a group of 7 species satisfying requirement (1). If species H is omitted, only 7 species are left. Because the species were put

in order in terms of the number of other species with which they had affinity, the species beyond H will either have the same number of affinities as H, in which case they are also potential members of a group of 7 species, or fewer affinities than H, in which case they cannot be included in a group of 7 species satisfying requirement (1). If species H had had affinities with 7 other species, the largest potential group would have contained the first 8 species, A to H.

[$X > V + 2$] If this is true, the largest potential group will contain the $X - 1$ species preceding the last one counted. For example, if species H had had affinities with 5 or fewer other species, the largest potential group would have been composed of the 7 species, A to G, for H and any species beyond it could only form a group containing 6 or fewer species.

The counting procedure thus selects those species which are potentially members of a group satisfying requirements (1) and (2). These must be further examined to determine whether such a group can be formed. Two preliminary tests of the possibility of its formation can be applied.

The first test can be stated as follows: In order to form a group of Z members from V potential members, there must be at least Z of these with more than $Z-2$ affinities with others of the potential group. For this test the affinities of each of the selected species with all others of the potential group are tabulated. This tabulation for the example is shown below:

Species	A	B	C	D	E	F	G	H	$V = 8$; $Z = 7$.
Affinities	7	6	6	6	4	4	4	5	

There are only 4 species which have more than 5 affinities and, therefore, a group of 7 species cannot be formed.

Passing the preceding test is a necessary but not sufficient condition for the formation of a group as can be seen by consideration of the following: If the interrelationships among the 8 potential members had been such that there was affinity between all species except the four pairs, A-B, C-D, E-F, and G-H, the tabulated affinities would have all been 6 and yet no group containing 7 species and satisfying requirement (1) could have been formed. On the other hand, if the species A to G had had affinity with all others except H, the tabulated affinities would have been seven 6's and one 0 and a recurrent group of 7 species could have been formed. In general, the affinities lacked by the species needed to form the group must be accounted for by species which are not necessary for its formation.

The second test determines whether this condi-

tion is met. It can be expressed algebraically as follows: In order to form a group of Z members from V potential members the following inequality must hold:

$(V - 1) (2Z - V) < 1 + \Sigma Z$ largest affinities $-\Sigma$ the rest of the affinities. Applied to the two cases discussed in the preceding paragraph, it gives the following results:

$(8 - 1) (2[7] - 8) < 1 + 7(6) - 1(6)$;
incorrect, a group of 7 cannot be formed.

$(8 - 1) (2[7] - 8) < 1 + 7(6) - 1(0)$;
correct, a group of 7 can be formed.

This is a necessary and sufficient condition for the formation of a recurrent group when $V = Z$ or $Z + 1$; it is necessary but not sufficient when $V = Z + 2$ or more for in this case the two sums on the right hand side of the expression can vary independently to some extent, the more so as there are more possible pairs of species within the category "rest."

Although passing these tests does not make the potential group a certainty in all cases, the two tests will prevent unnecessary work in many instances in which no group can be formed.

Returning now to the example, no group of 7 species could be formed so the possibility of the next smaller group, 6 species, is investigated. Two additional species, J and K, must now be considered for, having affinities with 5 other species, they could be members of a group of 6. The affinities within the group of 10 species are shown in the first line of the tabulation below. Both tests indicate that it may be possible to form a recurrent group of 6 species: there are over 6 species with more than 4 affinities; $(10 - 1) (2[6] - 10)$ is less than $1 + (9 + 8 + 8 + 7 + 5 + 5) - (5 + 5 + 4 + 4)$. The affinity interrelationships must now be examined in detail in order to make the final determination. Perhaps the easiest way to do this is to eliminate those species which do not have more than $Z - 2$ affinities, G and K in the example; repeat the tabulation as shown in the second line below, eliminate species which now do not have more than $Z - 2$ affinities and repeat until no more species can be eliminated. If at the end of this process V is less than $Z + 2$, the second test can be applied as a both necessary and sufficient condition for the formation of a recurrent group.

Species	A	B	C	D	E	F	G	H	J	K	
Affinities....	9	7	8	8	5	5	4	5	5	4	$V = 10$; $Z = 6$
	7	6	7	6	5	3	5	5	5	5	$V = 8$; $Z = 6$
	6	6	6	6	5	.	4	5	.	.	$V = 7$; $Z = 6$
	5	5	5	5	5	.	.	5	.	.	$V = 6$; $Z = 6$

In the last line $(6 - 1)(2[6] - 6)$ is less than $1 + 6(5) - 0$ and as $V = Z$ this is a necessary and sufficient condition for the formation of a recurrent group. Therefore, the species A-E, J constitute the group. The presence of J in the group emphasizes the necessity of considering all species which, on the basis of the number of other species with which they have affinities, might be part of the group. The initial counting procedure takes care of this automatically for the largest potential group, but the appropriate species must be added if this group cannot be formed and the next smaller must be considered. As there were no alternative groups of 6 satisfying requirements (1) and (2), requirements (3) and (4) do not have to be considered.

The species not included in the group are now examined to see if any have affinities *only* with members of the recurrent group. This is true of L and Q. Such species are considered associates of the recurrent group.

The procedure is repeated on the remaining species, omitting their affinities with members of the first recurrent group (Table II). The largest potential group contains 4 species; $X = 4$ and $Y = 3$ at species N. When the affinities within this group of 4 are tabulated, however, P and N have only 2 and a group of 4 species cannot be formed. All 7 of the species must be included when the next smaller group, 3 species, is considered. None can be eliminated on the basis of the first test and as $(7 - 1)(2[3] - 7)$ is less than $1 + (5 + 4 + 4) - (3 + 2 + 2 + 2)$ a group may be possible. When the interrelationships are examined in detail, the following groups are found to satisfy requirements (1) and (2): FGN, FGP, FHP, FKP, GMN. Requirement (3) will be satisfied if GMN and either FHP or FKP are selected. In order to decide between the latter two, the original sampling results would have to be investigated on the basis of requirement (4). It will be assumed here that FHP occurred as a unit more often than did FKP. The relation-

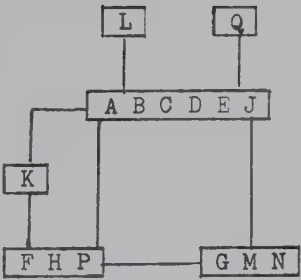


FIG. 1. Relations between recurrent groups.

ships between the species might be set out as shown in Figure 1.

This method has been applied to several studies reported in the literature and to an unpublished survey of the invertebrate fauna of decaying wood done by the author. In all cases the groups determined were consistent with what was known of the species' requirements, preferences, etc. The invertebrates from decaying wood were grouped using code numbers for the species in order to eliminate the possibility of bias; the groups found were in general agreement with impressions gained during sorting and counting.

ANALYSIS OF RECURRENT GROUPS

Recurrent groups based on the index of affinity proposed in this paper and determined by the procedure outlined above are composed of species which very frequently form a part of each other's biological environment. Such interspecific concepts as dominance, concordance and correlation should, therefore, be particularly meaningful when examined within these groups. The several methods of analysis suggested below use ranking procedures which, as Kendall (1955) has shown, are very useful for detecting general trends in material which includes some extreme values, as sampling results from natural populations nearly always do.

Before the analytical methods can be applied, samples representative of each recurrent group must be selected. For groups containing only a few species, selection can be based on the requirement that all species in the group are present in the sample. For groups containing many species, this may too greatly reduce the number of samples and some compromise must be accepted. The requirement should be set at a high percentage present but the exact value to be used will depend on the sampling results which are available. It should be explicitly stated in any case.

Table III presents some sampling results, related to actual observations but somewhat modified in order to show the different results which

TABLE II. Affinity between pairs of species (first recurrent group removed)

	SPECIES							Number of affinities
	F	G	P	N	H	K	M	
F								
G	+		+	+	+	+	+	5
P	+	+		+	+	+	+	4
N	+	+	.		+	+	+	4
H	+	.	+	.		.	.	3
K	+	.	+	.	.		.	2
M	.	+	.	+	.	.		2

+ = affinity; . = non-affinity

TABLE III. Number of individuals found and rankings

Species	SAMPLES									
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
A	124	28	9	5	10	24	4	2	5	3
B	15	1	21	5	1	13	85	7	26	1
C	30	217	101	112	175	287	87	19	133	85
D	2	3	8	8	14	18	10	1	15	11
E	55	42	6	7	62	117	3	8	71	136
J	2	9	3	8	24	11	2	2	8	1

(Ranking within samples)

A	1	2	3	2½	2	2	3	3	3	2	Sums of ranks
B	3	3	2	2½	3	3	2	2	2	3	23½
C	2	1	1	1	1	1	1	1	1	1	25½
D	2	2	1	1	2	2	1	2	2	2	17
E	1	1	2	2	1	1	2	1	1	1	13

(Ranking within species)

A	1	2	5	6½	4	3	8	10	6½	9	Sums of ranks
B	4	9	3	7	9	5	1	6	2	9	
C	9	2	6	5	3	1	7	10	4	8	
D	9	8	6½	6½	3	1	5	10	2	4	
E	5	6	9	8	4	2	10	7	3	1	
J	8	3	6	4½	1	2	8	8	4½	10	
	36	30	35½	37½	24	14	39	51	22	41	

may be obtained by the analytical procedures. Species A, B and C are poduromorph Collembola, D and E are small oribatid mites and J is a parasitid mite.

DOMINANCE

Numerical dominance is often expressed as a mean percentage of total individuals, obtained from the summed percentages of the samples considered separately. Such an expression, using percentages calculated for samples with different total numbers of individuals, is hard to interpret and gives no information about the constancy of the relation. The difficulties of interpretation are increased if the species are dissimilar in size, activity, etc. It is, therefore, suggested that determinations of dominance be restricted to species within recurrent groups which are, or appear to be, similar in regard to size, activity, food requirements, etc. and that the determination be based on ranks within samples, summed over the set of samples. This is equivalent to n things (species) ranked m times (number of samples in the set). The concordance among the rankings can be tested by the statistic W (Kendall 1955, pp. 94-102), which can range from 0 to 1; from no agreement to perfect agreement among the rankings. Details of the calculation of W and of an F -test of its significance are given in the Appendix. The use of ranks within samples gives every sample an equal voice in the decision and eliminates the

bias which one or two samples with exceptionally large or small percentages may impose on the per cent method.

Rankings within samples for the species A, B and C and D and E are shown in the second part of Table III.

For A, B and C: $n = 3$ and $m = 10$;

$$W = 123.5 / \left[\frac{100}{12} (24) - 10(.5) \right] = 0.633;$$

$$F = [(10 - 1)(.633)] / .367 = 15.52, \\ [n_1 = 1.8; n_2 = 16.2].$$

The value of W is significant at the .01 level showing that there is concordance among the samples; i.e., the dominance relations between the species tend to be constant over the set of samples. The sum of ranks is for each species the best estimate, in the sense of least squares, of the over-all rank of that species and if there is significant evidence of concordance the species may be ordered by these sums. The results may be stated as $C > A, B$; i.e., C is constantly dominant to A and B, and A is probably dominant to B but their sums of ranks are so nearly equal that the relative positions are less certain.

The value of W [$W = 0.04$; $F(n_1 = 0.8; n_2 = 7.2) = 0.375$ ($p > .20$)] is not significant for D and E indicating that dominance relation between these two species is not constant.

Relative Abundance

Relative abundance over all the samples is related to but not the same as numerical dominance. For example, assume that the numbers of individuals of two species found in 10 samples were as follows:

x	2	4	6	8	10	12	14	16	18	20
y	1	3	5	7	9	11	13	15	17	19

Species x would be found to be constantly dominant to species y and yet their relative abundances would not be significantly different. The difference between the relative abundances could be tested by the usual t -test of the difference between the means, but if there were any outsize samples they would exert a disproportionate influence. As these are often present among samples taken from natural populations, it is probably better to use the distribution-free statistic U and a t -test based on it (Hoel 1954, pp. 291-3). This tests the hypothesis that the distributions of the two populations of values are the same against the alternative that one distribution is situated to the left (lower valued) of the other. It is not affected by outsize samples. Details of the calculation will be found in the Appendix.

In the case of species A and B the observed

value of U is not significantly different from the expected value. There is, therefore, no evidence that the distribution of abundances of A was different from that of B . As is apparent by inspection, C was significantly more abundant than either A or B .

For D and E (D distribution assumed to be lower valued) :

$$\begin{aligned}\text{Exp. } (U) &= [10(10)]/2 = 50; \text{Var. } (U) = 175; \\ \text{Obs. } (U) &= 100 + [10(11)]/2 - 127.5 = 27.5 \\ t &= [27.5 - 50]/13.23 = -1.701 \\ [p(\text{one-tailed}) \sim .045].\end{aligned}$$

The observed value of U is significant at the .05 level, indicating that E was significantly more abundant than D even though determination of dominance had shown that it was not constantly dominant to D .

Concordance

The concordance among the species of a recurrent group on what constitutes a good habitat can be tested by the same methods (W) as were used in examining numerical dominance except that in this case ranking is done within species and the meaning of n (number of samples in the set) and m (number of species) are the reverse of those used in the previous test. If the observed number of individuals of a species is taken as an estimate of the goodness of a sample for that species, the samples can be ranked in regard to each species; this eliminates difficulties due to differences between species in average abundance, efficiency of collection, etc. The sum of these ranks over all species of the group is for each sample the best estimate, in the sense of least squares, of the rank of that sample among the samples selected as representative of the group. If there is significant evidence of concordance, the samples can be put in order.

Rankings within species are shown in the third part of Table III.

For the recurrent group considered as a unit; $n = 10$ and $m = 6$;

$$W = 1031.5 / \left[\frac{36}{12} (990) - 6(5.5) \right] = 0.351$$

$$F = [(6 - 1) (.351)] / .649 = 2.71, \\ [n_1 = 8.7; n_2 = 43.3].$$

The value of W is significant at the .05 level showing that there is agreement among the species on what constitutes a good or bad habitat. The samples can be put in order of decreasing goodness as follows: $6 > 9, 5 > 2, 3, 1, 4, 7, 10 > 8$. An examination of the other characteristics of these samples, especially the extremes, might reveal a

good deal concerning the preferences and requirements of the group as a whole.

Correlation

Rank correlations between species should also be calculated because the preceding generalization may miss significant relations: if, in a group consisting of four species two rankings are alike and the other two are exactly the opposite, the concordance will be zero although the six possible pairs of species will give four perfect negative correlations and two perfect positive correlations. Because of the possibility of parent correlations, nonsense correlations, etc., the interpretation of correlation analysis must always be viewed with reservations. If, however, correlation coefficients are calculated only for those pairs of species for which there are other reasons for expecting interrelationships, they may serve as useful guides to the mature and constancy of the relations. Kendall's (1955, pp. 34-8, 55) τ_b is probably the most convenient to use. Details of calculation and testing for significance are given in the Appendix.

This coefficient has been calculated for the three possible pairs of poduromorph Collembola (AB, AC, BC), for the pair of oribatid mites (DE) and for each of the Collembola with their possible predator, the parasitid mite (AJ, BJ, CJ). Only two coefficients are significant:

$$AC: \tau_b = +0.494; t = 1.885 (p \sim .06).$$

$$CJ: \tau_b = +0.768; t = 2.94 (p \sim .003).$$

The nearly significant positive correlation between the two species of poduromorph Collembola, AC, might be due to chance, might indicate that the species have a favourable effect on each other, or might result from their liking the same conditions and not interfering. The significant positive correlation shown by the presumed prey-predator pair, CJ, indicates that the predator did tend to congregate in those places where its prey was abundant. The absence of significant negative correlation between similar species means that in none of the pairs of species was an increase in the number of individuals of one always accompanied by a proportionate decrease in the number of individuals of the other. More evidence than the presence or absence of correlation is necessary before biological relationships can be claimed, but such an analysis will suggest those which might best repay further investigation.

DISCUSSION

This paper presents a defined, repeatable method for grouping together species which are frequent components of each other's biological environment. Such a method makes it possible to compare

groups found in different habitats or at different times or localities. As the composition of these recurrent groups is influenced by the method of sampling used and by the "level of significance" required of the index of affinity, the groups are abstractions. It has, however, been found that if sampling is related to the size, activity, etc., of the organisms and the significance requirement is made stringent, the groups formed have ecological unity in the sense of significant intragroup agreement on what constitutes a good or bad habitat. It seems reasonable, therefore, to consider them as natural assemblages, somewhat artificially delimited but nonetheless real.

Because the recurrent groups are composed of species which very often occur together, they represent particularly appropriate units within which to examine interspecific relationships. The analytical procedures suggested for this examination have two purposes; the provision of a summary description of relationships and the suggestion of working hypotheses upon which to base further field and laboratory work. The use of methods employing ranking gives each species an equal voice in the analyses, removes many of the difficulties due to non-normality of distributions and makes it possible to determine the constancy of general trends.

SUMMARY

A new index of affinity between species, based on presence and absence, is proposed and a table is provided from which the significance of an observed number of joint occurrences can be estimated.

Using this index and a four-part definition of a recurrent group, a procedure is outlined which leads to the largest, most frequent, separate groups within which all species formed a nearly constant part of each other's biological environment.

Ranking methods are suggested for the examination of interspecific concepts such as numerical dominance, relative abundance, concordance and correlation within these groups.

APPENDIX

Mathematical Methods

The essentials of the methods of testing for con-

$$\tau_b = \frac{2S}{\sqrt{[n(n-1) - \sum_t t(t-1)][n(n-1) - \sum_u u(u-1)]}}$$

The variance of S for $n \geq 10$ is given by:

$$\text{Var. } (S) = \frac{n(n-1)(2n+5) - \sum_t t(t-1)(2t+5) - \sum_u u(u-1)(2u+5)}{18} + \frac{[\sum_t t(t-1)(t-2)][\sum_u u(u-1)(u-2)]}{9n(n-1)(n-2)} + \frac{[\sum_t t(t-1)][\sum_u u(u-1)]}{2n(n-1)}$$

cordance (W) and correlation (τ_b) and of the U test are given below for the convenience of those to whom the texts may not be readily available. The expressions given for the first two tests include the corrections required when tied ranks are present. In both cases, t or u represent the extent of ties present; e.g., if a ranking has 2 members with one rank and 3 others with another rank, the summation is $2(4-1) + 3(9-1)$ in the case of W and $2(2-1) + 3(3-1)$ in the case of τ_b . For the calculation of W all ties are considered together; for the calculation of τ_b the extent of ties in one ranking is represented by t and that in the other by u . When tied ranks are absent, the summations are 0 and the expressions are considerably simplified.

Concordance (Kendall 1955): If n things are ranked m times, the ranks for each of the n things are summed and the sum of the squares of the deviations of these sums from their mean is represented by S , the concordance between the rankings (W) is given by the following expression:

$$W = \frac{12S}{m^2n(n^2-1) - m\sum_t t^3 - 1}$$

The significance of W can be tested by:

$$F = \frac{(m-1)W}{1-W}$$

$$[n_1 = n - 1 - \frac{2}{m}, n_2 = (m-1)n_1]$$

This does not have to be modified for tied ranks unless the number and extent of ties is large. To determine significance the usual table of the variance ratio (F) is entered with degrees of freedom n_1 and n_2 .

Correlation (Kendall 1955): The rankings are arranged so that one is in the natural order—1, 2, 3, . . . n . Following this arrangement, scoring is based entirely on the other ranking. Starting with the lefthand member, +1 is scored for every larger rank and -1 for every smaller rank to the right of it. After this has been done for each member of this ranking, τ_b is calculated from the sum of the scores (S) as follows:

$$2S$$

To test the significance of an observed S , the following expression may be taken as a normal deviate with mean 0 and unit variance:

$$t = \frac{|S| - 1}{\sqrt{\text{Var.}(S)}}.$$

U-test (Hoel 1954): If $x_1, \dots, x_n$ are members of one population and $y_1, \dots, y_m$ are those of a second, the following expressions give the expected and observed values of U and its variance.

$$E(U) = \frac{nm}{2}, \text{ Obs. } (U) = nm + \frac{m(m+1)}{2} - T, \text{ Var. } (U) = \frac{mn(m+n+1)}{12}$$

T is the sum of ranks of the y 's when the x 's and y 's are ranked together. These expressions can be used in a one-tailed t -test of the hypothesis that the distributions of the two populations are the same against the alternative that the x population is situated to the left (lower valued) of the y population. For m and n equal to 8 or more, the following expression may be taken as a normal deviate with 0 mean and unit variance:

$$t = \frac{\text{Obs. } (U) - E(U)}{\sqrt{\text{Var. } (U)}}.$$

This test is nearly as efficient as the usual t -test when applied to normally distributed populations; as it is distribution-free, it is applicable to non-normal distributions.

TABLE I. Minimum values of J which are significant at the .05 level

nB/nA	1.0	1.5	2.0
nA			
5.....	5	5	
6.....	5	6	
7.....	6	7	6
8.....	7	8	7
9.....	7	8	8
10.....	8	9	9
20.....	14	16	10
30.....	19	22	17
40.....	25	29	24
50.....	29	35	32
60.....	36	42	39
70.....	41	48	46
80.....	46	55	53
90.....	52	61	59
100.....	57	67	67

nA =total number of occurrences of species A ; nB =same for species B ; $nA \leq nB$ by definition; J =number of joint occurrences.

Example: If $nA=20$ and $nB=30$, a J of at least 16 is necessary for significant evidence of affinity; if $nA=25$ and $nB=35$ ($nB/nA=1.4$), minimum significant J can be estimated as

$$16 + \frac{22-16}{2} \cdot \frac{1}{5} \left[\left(16 + \frac{22-16}{2} \right) - \left(14 + \frac{19-14}{2} \right) \right] = 18.5.$$

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THE EFFECTS OF LIGHT AND TEMPERATURE ON THE FECUNDITY OF THE GREENTHROAT DARTER, *ETHEOSTOMA LEPIDUM*¹

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INTRODUCTION

The greenthroat darter, *Etheostoma lepidum* (Girard), is known only from the Edwards Plateau in habitats described in a later section (Hubbs 1954). Its geographic range approximates the extent of the Balconian Biotic Province of Blair (1950).

As the greenthroat darter inhabits clear spring-fed waters which were thought to have little or no temperature variation the senior author thought that it would be an excellent animal on which to study the effects of light.

HABITAT OF GREENTHROAT DARTER

In nature *E. lepidum* is found in many habitats. Specimens have been collected over bottoms ranging from bedrock through gravel to silt. They have also been collected in dense vegetation and in almost entirely denuded areas. They have been taken from both quiet and rapid water. The largest populations, however, have been found in riffles with rocks from 2 to 8 inches in diameter covered with aquatic plants. Within the range of its near relative, the orangethroat darter, *E. spectabile* (Agassiz), the greenthroat darter is more closely restricted to vegetation. The greenthroat darter occurs in shaded and unshaded streams. It has never been taken from water that is more than slightly turbid. Extreme temperatures at collection stations containing *E. lepidum* ranged seasonally from 7° to 35° C; most station water temperatures ranged from 14° to 24° C.

EGG DEPOSITION

The greenthroat darter has adhesive eggs that are heavier than water. When a female in an

aquarium becomes ripe, the males begin to court her. The relationship between sexes during spawning activity is promiscuous. The eggs of each spawning, which are laid in several groups, are usually fertilized by the largest male in the tank. In aquaria with vegetation (and probably in nature) the eggs are attached to the vegetation, with an apparent preference for filamentous algae. Most of the eggs in our laboratory are laid in glass wool covering submerged activated charcoal filters. When eggs are laid in these aquaria, the spawning pair is in an upright position. If aquatic vegetation and glass wool are absent, females lay eggs on any solid object, often on the sides and in the corners of the aquarium above the bottom. When eggs are laid in aquarium corners, the spawning pairs have their heads pointed upward. In an aquarium provided with an inside surface filter made from a plastic garbage strainer, the underside of the filter is a favorite egg deposition site. The pair spawns upside down under the filter. As the eggs rarely adhere to the plastic, the importance of this site was not realized until actual spawnings were observed. Thus, the tops of objects below the filter may prove not to be spawning locations but rather catchment spots for falling eggs. The allopatric Rio Grande darter, *E. grahamei* (Girard), will lay eggs on the underside of rocks less than 30 mm off the bottom (Strawn 1955-1956) but greenthroat darters have only laid under rocks which are much farther above the bottom. All or part of the lower surface of a rock may be a distance above the bottom due to the configuration of the rock or the bottom. In nature the undersides of rocks may be an important spawning site. Thus under different conditions the same spawning pair may exhibit three of the egg deposition types for darters discussed by Winn (1954).

FIELD OBSERVATIONS

The breeding condition of greenthroat darters has been observed repeatedly in the field. Two stations from the Guadalupe River drainage have been studied repeatedly and observations on breeding conditions recorded sixteen times. Other stations in the same drainage have also been repeated as often but the greenthroat darter is absent or so rare that a continuous series of obser-

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vations is not available. Because the light conditions are similar and the temperature conditions differ it is possible to determine which has the greater effect under natural conditions.

Station 1. South Fork of the Guadalupe River at C. L. Secor's Lynxhaven resort eight miles southwest of Hunt, Kerr County, Texas. The station extends from an eight-foot cement and stone dam downstream 100 yards across State Highway 39, for 35 yards through a plant-covered riffle shaded by pecan trees. The region between this station and the headsprings is impounded and observations on the greenthroat darter are difficult. Through most of this station the stream flows over a bare limestone flat; however, the majority of the darters have been collected from the shaded area immediately below the dam or the shaded riffle below the highway bridge. Greenthroat darters do occur in the barren segment, perhaps due to the scarcity of orangethroats in the area. Dense growths of aquatic vegetation occur on the sides, especially in the locations from which the darters have been collected. Occasionally large amounts of decaying plants accumulate throughout Station 1 after being removed from the upstream impoundment. The other fish species occurring at this station are those listed by Hubbs, Kuehne, and Ball (1953) for this region. Although streams flowing over bare limestone flats often have extreme local temperature variations, temperatures at this locality are relatively consistent due to the large volume of water flowing over the exposed rock. As the water is near its spring source, seasonal temperatures do not vary greatly. The extreme recordings differ by 10° C.

Station 2. Guadalupe River, east of a low water bridge (which in effect is a low dam) on a road from State Highway 39 to Camp Rio Vista, 3.5 miles east of Hunt. The station covers the entire riffle east of the bridge. Two major channels diverge below the bridge and join in the downstream segment of the riffle. Several other small channels flow through the region. Many rapid-water habitat types occur in the station. Two of these have yielded most of the greenthroat darters. One is a Potamogeton bed in the northern channel, 30-40 yards east of the bridge, and the other a bed of *Myriophyllum exalbescens* Fernald in the southern channel 70 yards east of the bridge. Other habitats have less vegetation and orange-throat darters outnumber greenthroats. Most of the station is shaded by cypress trees. The other fish species occurring at this station are those listed by Hubbs, Kuehne, and Ball (1953) for this region. Streams flowing over cypress-shaded riffles do not have extreme local temperature vari-

ations. No significant local midstream temperature variations have been noted at this station after water flowing over the bridge has been mixed in the current. Water at this location is farther from its spring source than at Station 1, thus seasonal temperatures vary more widely. The extreme recordings differ by 21.5° C.

Observations on the breeding condition of greenthroat darters at Stations 1 and 2 have been made between June 1953 and July 1956. Water temperature, season, and breeding condition of greenthroat darters are plotted in Figure 1. As no appreciable difference was noted the data for the three years are not separated by year. At Station 1 ripe males and females were observed at all dates except for two in July. During one of the July collections with no ripe females, ripe males were collected. One ripe female and two ripe males were noted in a collection made on July 17, 1956. The female and one of the ripe males were collected on the open flat near the dam, where the water temperature was 24.6° C. The other ripe male was collected with many non-ripe adults east of the highway bridge, where the water temperature was 25.4° C. It is possible that on other sampling dates some non-collected males and/or females were ripe. Most of the collections from Station 1 contain young. As ripe females are seldom taken in July it is not surprising that no young were taken in the August collection. Thus greenthroat darters breed for 10 to 12 months at Station 1.

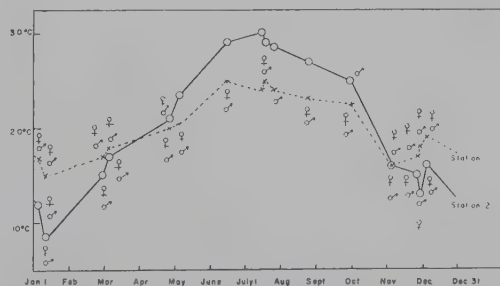


FIG. 1. Correlation of season and temperature with reproductive condition of greenthroat darters at two stations in the Guadalupe River drainage. Symbols by sampling dates show sex(es) in breeding condition.

At Station 2 ripe males and females were taken only from November through April. Some of the adults taken in the November 7th collection were not in breeding condition. Only a few males were ripe on October 2nd. Thus the breeding season at Station 2 is no longer than six months, four to six months shorter than at Station 1.

Chemical conditions at the two stations are similar. The biologic communities do not differ greatly. Available food at the two stations is adequate as most darters appear well fed. One exception is Station 1 shortly after the upstream impoundment was drained, thus scouring the sample area. The food deficiency could shorten the reproductive period at Station 1; however, Station 1 has the longer reproductive period. The duration of daylight does not vary greatly between the two stations less than 15 miles apart. Therefore the only major difference between the stations is in temperature variations. These temperature variations appear to limit the reproductive period of greenthroat darters in nature.

Some of the temperatures at Station 1 when ripe fish were observed exceeded those at Station 2 on other dates when no ripe fish were observed. Much of this may be due to diel temperature changes as all but the June and July observations were made between 8 and 11 A.M. It is likely that afternoon water temperatures are higher, especially at Station 2. Thus, the apparent discrepancy may be artificial. Moreover, fish will maintain ripe gametes at high temperatures for short periods, but need more than one week at low temperatures to ripen eggs. Deviations from the expected conditions may result from short-term temperature fluctuations.

Greenthroat darters from other spring areas are ripe during summer months when downstream populations from the same stream are not ripe.

Observations at Station 2 have been slightly complicated by periodic environmental sexual separation. At times during intensive reproductive activity over two-thirds of the females are found in the Potamogeton bed and more than three-fourths of the males in Myriophyllum. Fahy (1954) also suspected that selection of different habitats by the sexes and differential sampling of the habitat may be the cause of sex ratios differing from 1:1, as reported for greenside darters, *Etheostoma blennioides* Rafinesque (Lachner, Westlake, and Handwerk 1950) and listed in a table for johnny darters, *Etheostoma nigrum* Rafinesque (Raney and Lachner 1943). Likewise sex-ratio differences in age-group I greenside darters reported by Fahy (1954) may result from differential selection of the habitat.

LABORATORY EXPERIMENTS

Individuals from many greenthroat darter populations have been bred in the laboratory. Under favorable food and temperature conditions most males are ripe whenever tested. Under similar conditions females possess mature eggs every

four to ten days depending upon temperature (Strawn and Hubbs 1956). None of the populations appears to be affected by light duration or duration of spawning interval. Within the limits used, we have not noted any effect from varied light intensity.

A number of light-control experiments have been carried out using individuals collected at field observation Station 2. Illumination was by 15 watt 4500° white Sylvania fluorescent lights controlled by automatic timers. The lights were in "full aquarium" covers. All aquaria were 2 x 1 x 1 foot, with a layer of limestone and sand one half to three-quarters of an inch thick on the bottom. No higher aquatic plants were in the aquaria. The sides of the aquaria were covered with one or two layers of aluminum foil. Layers of black-out cloth were draped over the aquarium covers to prevent light entering around the cover. To test the effectiveness of this device, one of the light-sealed aquaria was placed in a dark room and its light turned on. No light was observed from the outside. Temperatures and egg counts were taken daily (usually between 7 and 9 A.M.).

In the first set of experiments the eggs laid on the aquarium sides were counted and knocked to the bottom. From March 13 through 28, 1956 twelve aquaria containing four pairs of fish conditioned to laboratory life were used. Two each were held at 0, 8, 12, 16, 20 and 24 hours light per 24 hours (Table I). It soon became apparent that both temperature and light varied in this experimental design. Although there is a correlation between large number of eggs and the least amount of light, egg counts are much better correlated with temperature than with light duration. The coolest aquarium (0 hours light, 23.72° C)

TABLE I. Egg production of *E. lepidum* with many females in each aquarium

	No. hours light...	0	8	12	16	20	24
March 13-28...	Total eggs	51	7	75	19	0	0
4 pairs.....	Eggs per female day	0.80	0.11	1.17	0.30	0.00	0.00
	Average temp.	23.89	25.83	25.28	25.50	27.22	26.78
March 13-28...	Total eggs	271	6	16	2	24	1
4 pairs.....	Eggs per female day	4.23	0.09	0.25	0.03	0.38	0.02
	Average temp.	23.72	25.67	25.11	26.33	25.72	26.94
March 31-							
May 14.....	Total eggs	129	339	526	236	392	579
5 pairs.....	Eggs per female day	0.67	1.51	2.34	1.05	1.74	2.57
	Average temp.	21.06	21.28	21.22	21.28	21.17	21.39
		to 24 hours light	to 16 hours light	to 20 hours light	to 8 hours light	to 12 hours light	to 0 hours light
May 15-							
June 18.....	Total eggs	44	67	22	196	16	23
5 pairs.....	Eggs per female day	0.26	0.39	0.13	1.15	0.09	0.14
	Average temp.	24.67	24.72	24.61	24.67	24.67	24.55

TABLE II. Egg production of *E. lepidum* with one pair in each aquarium.

	No. hours light	0	8	12	16	20	24	
1954 July 6- Sept. 3	Av. temp. No. eggs No. spawnings No. eggs per spawning No. days between spawnings	19.55 1556 12 129.7 5.00	19.55 2774 ¹ 11 252.2 5.00	19.18 480 ² 4 120.0 6.67	20.37 470 ³ 2 235.0 4.00	19.81 822 10 82.2 4.67	19.44 3002 13 230.9 4.50	19.57 2302 13 177.1 4.50
Sept. 14- Nov. 15	Av. temp. No. eggs No. spawnings No. eggs per spawning No. days between spawnings	16.80 512 3 170.7 9.00	15.71 182 ⁴ 2 91.0 7.00	16.04 375 ⁴ 3 125.0 7.00	 415 ⁵ 3 138.3 5.50	15.78 448 4 112.0 5.00	17.06 514 ⁶ 3 171.3 10.00	16.53 1996 8 249.5 7.14
Nov. 16- Jan. 1	Av. temp. No. eggs No. spawnings No. eggs per spawning No. days between spawnings	20.37 1606 7 229.4 6.17	20.25 310 ⁷ 4 77.5 4.75		20.39 603 ⁸ 4 150.8 4.00	20.22 184 ⁹ 2 92 4.00	20.61 242 4 60.5 5.33	20.44 2528 10 252.8 4.44
1955 Jan. 3- Mar. 7	Av. temp. No. eggs No. spawnings No. eggs per spawning No. days between spawnings	17.73 508 ¹⁰ 3 169.3 6.00	18.33 215 3 71.7 6.00	18.24 190 6 31.7 6.20	18.26 436 ¹¹ 9 48.8 4.50	18.49 143 3 47.7 4.00	18.09 284 6 47.3 6.50	18.06 2815 ¹² 12 234.6 5.91

¹Female laid 100 more eggs 7 days later, died 3 days later.²Female laid another egg 10 days later, died same day.³Female laid 21 more eggs 7 days later, died one day later.⁴Same female used for both tabulations; did not lay eggs for 34 days between series.⁵Female died 3 days later, last spawning normal in number and time.⁶Fifteen day interval between first two spawnings, 5 days between second two.⁷Female laid 2 more eggs 6 days later, did not lay again, spawnings 125, 112, 25, and 48 eggs each.⁸Female laid 45 more eggs 8 days later, 1 egg 3 days later, did not lay again.⁹First laying 37 days after last laying of previous series, female swimming on side, obviously in old age, died 17 days after last spawning.¹⁰Female laid 31 more eggs 11 days later, died 15 days later.¹¹Spawnings in glass wool 83-100 eggs, on aquarium sides 16-51.¹²Female laid 141 more eggs 6 days later, died 2 days later.

produced more than one-half the eggs, the three warmest (both 24 hours light and one 20 hours light) produced only one egg. Although temperature is not perfectly correlated with egg counts, the variations can be attributed to chance. Apparently the upper limit of egg production is between 24 and 27° C, depending on the individual female.

Six aquaria were then immersed in refrigerated water baths to reduce temperature variations. Five pairs were placed in each aquarium. In the March 31 to May 14 series of experiments, only the 0-hour light aquarium differs markedly from the others. Most of the eggs in this tank were found during May, toward the end of the experimental period. As the fish in this tank came from one of the warm tanks in the previous experiment, the first month of the experiment may have been required to get the fish into breeding condition. The fish exposed to the other light duration came from the more productive aquaria. The temperature in the water bath was then raised about 3.5° C. The light period to which each aquarium was exposed was changed. No significant correlation between light duration and egg counts was noted. Only the 16-hour light tank differed markedly from the rest. As the 12- and 20-hour tanks (adjacent light durations) produced the fewest eggs, we believe that the high count is due to

chance. All of the tanks at the higher temperature had far fewer eggs than previously, undoubtedly due to a reduction in egg production above 23° C.

The number of eggs found in the bare tanks was far lower than that in tanks containing quantities of glass wool. Apparently some eggs did not adhere to the aquarium glass and dropped to the bottom where they were assumed to have been knocked off the sides previously. If greenthroat darters eat newly laid eggs, those exposed on the aquarium sides are more readily eaten. Nevertheless conditions in the tanks were similar, therefore comparison of the eggs found in the tanks without glass wool is considered valid.

The remaining experiments were carried out with one pair of fish per aquarium (Table II). Glass wool was placed on submerged activated charcoal filters. All but one female laid the bulk of her counted eggs there. One female in a 12-hour light aquarium laid many eggs on the aquarium. All of the fish except one 8-hour light pair were from Field Observation Station 2. Shortly after this series of experiments had begun, it was noted that the number of eggs produced by a female in one spawning (a spawning is considered to be all of the eggs in one female that ripen at the same time) was correlated with her size. The last spawning (or spawnings) of

a female often varies widely from the others in number of eggs and time between spawnings (footnotes on Table II). Where marked changes occur, the figures are not entered in the tabulations; however, the divergent spawnings are itemized in the footnotes. In none of the experiments is the number of eggs per laying apparently correlated with either temperature or light. Variations in the length of time between spawnings appear to be controlled by temperature.

Between July 6 and September 3, temperatures averaged about 19.5° C. For all fish that had more than four spawnings, eggs were produced every 4 to 5 days. The differences are not significant.

Between September 14 and November 15, temperatures averaged about 16.5° C. Spawnings were infrequent and female mortality high at these temperatures so the intervals between spawnings vary widely. There is no correlation between light duration and spawning frequency.

Between November 16 and January 1, temperatures averaged about 20° C. Only one tank, 0-hour light, had a noticeably longer interval between spawnings. As the 20-hour tank had the next longest interval, individual variation is suspected as the cause.

Between January 3 and March 17, temperatures averaged about 18° C. Although the interval between spawnings varied, no correlation with light duration is noted.

Only once in eight experiments is any possible correlation of egg production with light duration noted. As the results are not repeated, the occurrence is presumably due to other phenomena. Therefore experimental evidence and field data support the hypothesis that light duration has little effect on reproduction of greenthroat darters.

The experiments with single pairs were conducted from 15° to 20° C. Within this range the interval between spawnings (thus spawning rate) is inversely correlated with temperature. The average of the number of days between spawnings of all pairs was 7.2 (near 16.5° C), 5.6 (near 18° C), 4.9 (near 19.5° C) and 4.8 (near 20° C). Only one female was used in all four temperature ranges. Her average interval between spawnings was 7.14 (16.53° C), 5.91 (18.06° C), 4.50 (19.57° C) and 4.44 days (20.44° C).

All of the eight experiments indicate a correlation of egg production with temperature. The first four (Table I) indicate a decrease in egg production with increased temperature between 21 and 27° C. The last four (Table II) indicate a decrease in egg production with decreased tem-

perature between 16 and 20° C. Although other environmental factors cannot be discounted, it is possible that the temperature for maximum reproduction occurs near 20° C as two otherwise healthy females (Table II, footnotes 7 and 8) ceased laying at slightly higher temperatures. No other females in that sequence of experiments ceased laying for so long a period. The gradual reduction of egg production with increased temperature in the aquaria with four or five females reported in Table I may be due to cessation of reproduction in individual females.

More than 90% of the eggs in all spawnings were fertilized. Fertilization was approximately equal in all light durations.

DURATION OF REPRODUCTIVE PERIOD

One female exposed to 24 hours light is known to have been in breeding condition from July 6, 1954, to March 14, 1955, or 251 days (Table II). She regularly laid eggs during the non-tabulated interval between September 3 and 14. This female had been brought into the laboratory on or before February 28, 1954, in breeding condition. She died on March 16, 1955, from fungus. Dominant males are constantly nipping on the fins of other fish in the aquarium. When only one pair is isolated, the female receives the constant attention of the male and she cannot constantly avoid him in the confined quarters of an aquarium (Strawn 1955-1956). Therefore, many of the nipped and weakened females die of fungus. As the female was active until slightly before she succumbed to fungus, it is likely that she might have otherwise continued producing eggs for some time. The first recorded spawnings of this female contain more eggs than the number produced by some greenthroat darter females from this locality. As the number of eggs produced is correlated with size and therefore age, the female may have been producing eggs for a considerable period before precise counts were made. This hypothesis is supported by her known history. She was placed in one of the five experimental aquaria in which the greatest breeding activity occurred from March 13 to 28. From March 31 to May 14 she was in the 8-hour light aquarium and from May 15 to June 18 she was in the 16-hour light aquarium (see Table I for egg production in these aquaria). Many eggs were also found in this aquarium between June 18 and July 6. As this female was in aquaria in which many eggs were laid between March 31 and July 6, it is probable that she was in breeding condition over that interval. It is possible that she was in breeding condition during

her entire life in the laboratory. If so, she was producing eggs regularly from early November 1953 to March 14, 1955.

DISCUSSION

Greenthroat darters can be kept in continuous breeding condition in the laboratory. They will produce gametes under varied light conditions. We do not believe that light duration is a limiting factor in the reproductive activity of greenthroat darters.

Likewise we do not feel that the time of year has any direct effect on reproduction in greenthroat darters. In the laboratory they breed equally well at all seasons if other factors are similar. We have also maintained breeding populations of the orangethroat darter, *Etheostoma spectabile*, from the Guadalupe River at seasons when no natural reproduction is known at the collection localities.

We do not believe that laboratory conditions play a significant role in the experiments on greenthroat darters. Wild-caught females from other localities produce eggs at equal intervals to those produced by females conditioned to the laboratory.

Many populations (including that from Station 2) have bred in the laboratory when the fish in the source population were not in breeding condition. Some of these were collected at temperatures above those at which spawning occurs, and brought into breeding condition by lowering the temperature. The results of our work differ from those of Fahy (1954) who worked on the greenside darter, *Etheostoma blennioides*, from Salmon Creek, New York. He stated that 51° F (10.56° C) is the critical water temperature for the initiation of spawning; but this temperature, or a higher one, must be maintained for a few days. Winn (1954) and Lake (1936) also demonstrated minimum reproductive temperatures for northern darters. We found that reproduction of the greenthroats can be initiated by lowering the temperature.

Fahy also proposed that the number of yolked eggs (more than 0.10 mm) in a female at the start of a spawning season is the number she will lay in a given spawning season. When he tabulated measurements for ova in ovaries of greenside darters collected just before the breeding season started, few ova measuring 0.10 to 0.20 mm were recorded. As the number of ova in excess of 0.10 mm approximated the number of eggs laid during one spawning season in the aquarium by females of about the same size, he logically assumed that the spawning period was

terminated when all of the eggs were laid. Further confirmation of this conclusion was the similarity in the dates at which field and laboratory spawning stopped. Fahy did not conduct experiments to determine whether a high temperature would cause a cessation of spawning. The field temperatures listed by Fahy rose rapidly shortly before and after spawning ceased. Tabulation of egg measurements of greenthroat darters (Fig. 2) shows a log-normal distribution like those of Harrington (1948) and Clark (1925). Egg measurements were made following the techniques of Clark. Unlike Fahy we did not transfer the eggs to 70% ethyl alcohol before measuring. We find no scarce size class in small eggs. The only variation from a logarithmic curve is in the largest size categories when the eggs for an individual spawning mature together. This latter phenomenon was noted by Harrington and Clark as well as by Fahy. We find no temporal cause for termination of spawning activity.



FIG. 2. Size distribution of eggs in right ovary of 45 mm *E. lepidum* from Station 2 collected February 28, 1953.

We do not know whether the differences between Fahy's experimental results and ours are due to the different species used, different areas studied, or technique.

SUMMARY

This study has shown that the reproductive rate is controlled by temperature and the condition of the fish. In nature, mature fish are not ripe at extreme temperatures at seasons when nearby populations are in breeding condition at more favorable temperatures. Light duration and intensity do not appear to affect fecundity of greenthroat darters. No consistent differences were noted in laboratory experiments between fish exposed to different light durations held at approximately the same temperature. The fecundity varied with temperature in the experiments. The optimal temperature for egg production appears to be between 20 and 23° C. One female pro-

duced eggs in the laboratory at regular intervals for at least 251 days and possibly for as long as sixteen months.

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FIR-SPRUCE-BIRCH FOREST IN NORTHERN MINNESOTA

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A coniferous forest occupies northeastern Minnesota. The western part of the state is prairie. Between the coniferous region and the prairie is a narrow strip of deciduous forest (Fig. 1). This is the picture one gets from the published maps of Minnesota vegetation, either from Upham's original survey or maps adapted from his (Upham 1884, Rosendahl 1955, Daubenmire 1936, and Buell and Wilbur 1948).

Traveling through the region mapped as coniferous, one is impressed by considerable stretches of broadleaf forest. Much of this forest is dominated by trembling aspen (*Populus tremuloides*) and big-toothed aspen (*P. grandidentata*) which clearly are successional (Kittredge 1938) and there by virtue of the fire and lumbering history of the area. Yet there are frequent stands of deciduous forest dominated by sugar maple (*Acer saccharum*) and basswood (*Tilia americana*) which are not successional but are capable of maintaining themselves (Buell and Bormann 1955). In the latter, balsam fir (*Abies balsamea*) is commonly present either as a successful component (Grant 1934) or as a scarcely successful invader (Buell and Gordon 1945, Buell 1956).

Occurring frequently, however, is a coniferous forest community that appears capable of maintain-

ing itself. It is the fir-spruce-birch community and is similar to that described by Cooper (1913) as the climax forest of Isle Royale, Michigan. He found the fir to be by far the most abundant species, with white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*) of secondary importance.

The objective of this study was to gather data on the upland fir-spruce-birch community both in the Itasca Park area where it occurs in competition with maple-basswood forests and in northeastern Minnesota where the maple-basswood community is absent or, if present, highly restricted as to site. Stands were sought where the fir-spruce-birch community had been perpetuating itself for several generations with no evidence of a preceding community of different composition. From what is known of this community's ability to perpetuate itself (Cooper 1913), it was expected that such situations might exist. However, no such stands were found, since clear evidence of a previous pine stand was found in every case, and therefore those studied were merely the longest established and best developed that were located in the two areas.

Five stands were selected, two in the Itasca Park area near the Itasca Biological Station, and

three in the vicinity of Ely (Fig. 1). The former are designated as the Iron Springs and Lake Alice stands. The Iron Springs stand (Se. Sec. 28 T. 144 N. R. 38 W. in Clearwater County) was located on the upper part of a gentle north-facing slope, the lower part of the slope being occupied by a tamarack (*Larix laricina*) bog.



FIG. 1. Vegetation map of northern Minnesota showing location of the two areas in which the fir-spruce-birch stands referred to in this paper are located. 1. Itasca Park area, 2. Ely area. Unshaded portion = conifer region; solid shading = deciduous forest; stippled = prairie region.

The Lake Alice stand (Se. Ne. Sec. 15, T. 143 N. R. 35 W. in Hubbard County) was situated on a low hill surrounded by a black spruce (*Picea mariana*) bog.

The three stands in the Ely region were all in St. Louis County. They are designated as the Moose River, the Wilderness Center, and the Norway Island stands. The Moose River stand was located on the north side of Echo Trail west of where it crosses Moose River. In a region of rolling terrain, the stand (Sw. Sec. 10, T. 65 N. R. 14 W.) occupied the higher land but came in contact with bog forest in the lower areas. The Wilderness Center stand (Sw. Sec. 9, T. 64 N. R. 10 W.) was located on a bay of Basswood Lake west of the Wilderness Research Center, which is fifteen miles northeast of Ely (Ahlgren 1952). It was on a west-facing slope near the lake. The Norway Island stand was located on the island of that name in Basswood Lake. The island is very close to the Canadian border and is the site of a former trading post. The stand (Nw. Sec. 11, T. 64 N. R. 10 W.), located on relatively level terrain, was on the northeastern part of the island.

Geologically the Itasca and the Ely areas are very different (Leverett and Sardeson 1932). The Itasca area is underlain by deep deposits of glacial drift (gray drift of late Wisconsin, Manakato substage) which are highly calcareous. In

contrast, the Ely area is characterized by a predominance of glacial scouring resulting in shallow glacial deposits which are non-calcareous. The outcropping bedrock is also non-calcareous.

On the basis of available climatological data (Reichelderfer et al. 1941) there is no great difference between the two areas. The yearly rainfall is slightly higher at the weather station near Ely (22.68 inches at Itasca, 25.58 inches at Virginia near Ely), but the summer rainfall in the two places is almost identical (9.99 inches and 10.12 inches) for the three summer months. The July average temperatures are the same—66.8 degrees F. The most pronounced difference lies in the length of the growing season, there being an average of 99 days between killing frosts at Itasca and 111 days at Virginia (which is 50 miles southwest of Ely).

The authors wish to thank Mr. H. B. Hubachek who made available the facilities of the Wilderness Research Center at Basswood Lake and Mr. C. E. Ahlgren who helped to locate stands in that area.

The field work was accomplished as a part of the Itasca Biological Station Research Program during the summer of 1950.

METHODS

One stand in each region was studied in some detail and, to the extent that available time and small size of some of the stands allowed, information was gathered from limited sampling in others. In the Iron Springs stand the tree layer was sampled employing thirty 10 x 10 m. quadrats and 300 m. of transect line. Cover was measured along the transect lines (Buell and Cantlon 1950). In the Moose River stand thirteen quadrats and 140 m. of transect line were used. The sampling employed 6, 8 and 6 quadrats and 210, 80 and 60 m. of transect line in the Lake Alice stand, the Norway Island stand and the Wilderness Center stands respectively. Although the sampling of these latter was scarcely adequate from the point of view of detailed stand description involving all features, further quadrats and longer intercept lines could change the figures to only a minor extent in this rather uniform type of forest. The greatest influence of further sampling would undoubtedly be in the sapling size class of trees which were generally clumped in the openings where trees had fallen. All individuals of tree species over 1 ft. in height and less than 1 in. d.b.h. (diameter at breast height) occurring in the quadrats were counted and recorded as saplings. Seedlings (individuals of the species less than 1 ft. in height) were counted in the 1/2 x 2 m. quadrats set up for the study of the herb and moss layers.

The shrub layer was sampled by the line intercept method with only cover data being obtained. Transgressives of the tree species occupying this layer were included. The same transect line was used as for the canopy layer.

The herb and moss strata were sampled with $\frac{1}{2} \times 2$ m. quadrats located at 5 m. intervals along the transect lines. In these quadrats estimate was made of space unoccupied in each layer as well as per cent cover contributed by each species. The area occupied by fallen logs was also estimated.

Mechanical analyses of soils were made using the hydrometer method (Bouyoucos 1936).

Light readings were taken in the Iron Springs stand on a clear cloudless day between 12:30 and

1:00 P.M. The Weston illumination meter model 756 was used. The meter recorded 10,000 foot candles uniformly for ten consecutive readings outside the forest both before and after the readings in the forest. One hundred and four readings were taken at a height of six feet every meter along two of the transect lines.

Nomenclature follows Rosendahl (1955) for trees and shrubs, Fernald (1950) for all other vascular plants, and Grout (1940) for mosses.

RESULTS

Stands of the Itasca Park region

Iron Springs stand.—In the Itasca Park region the Iron Springs stand was one of the oldest and



FIG. 2. Tree cover and frequency by stands. Length of bar indicates % of total tree cover; width of bar, frequency of occurrence based on total number of quadrats per stand. For example at Iron Springs (I.S.) balsam fir represents 75% of total tree cover with 100% frequency. Species not occurring in quadrats or on transects indicated by x. Space represents openings in the canopy, in other words, the percent of unoccupied space in the tree layer. Abbreviations: I.S. = Iron Springs; L.A. = Lake Alice; M.R. = Moose River; W.C. = Wilderness Center; N.I. = Norway Island; Av. = cover and frequency averaged for the five stands.

TABLE I. Density (D) per 1000 square meters for two size classes (1-3.9 inches and 4-inches d.b.h. and over), and basal area (B.A.) expressed as percent total basal area of each stand. See Figure 2 for explanation of abbreviations of stand names.

	I. S.			L. A.			M. R.			W. C.			N. I.		
	D		B.A.	D		B.A.	D		B.A.	D		B.A.	D		B.A.
	1-3.9"	4" and over		1-3.9"	4" and over		1-3.9"	4" and over		1-3.9"	4" and over		1-3.9"	4" and over	
<i>Abies balsamea</i> (balsam fir)	28	85	79.8	200	121	81.0	235	1	25.4	83	95	73.3	24	58	85.4
<i>Picea glauca</i> (white spruce)	1	3	4.2	9	7	4.7	5	16	10.7	1	10.1	1	1	1	4.4
<i>P. mariana</i> (black spruce)	2	12	12.9				15	15	28.3						
<i>Betula papyrifera</i> (paper birch)	1	4	0.2		1	1.0	4	6	8.1	5	22	16.4	8	11	7.5
<i>Populus tremuloides</i> (trembling aspen)		1	0.6		5	11.0								3	1.8
<i>P. grandidentata</i> (large-toothed aspen)		1	0.5	1		0.7									
<i>P. balsamifera</i> (balsam poplar)				1	3	1.7									
<i>Fraxinus nigra</i> (black ash)		1	0.3							1		0.1			
<i>Sorbus</i> (mountain ash)		1	0.1				1		0.1			0.1	3	2	0.9
<i>Acer rubrum</i> (red maple)		1	0.1												
<i>Pinus resinosa</i> (red pine)		1	1.3												
<i>P. banksiana</i> (jack pine)							6	27.2							
Total B. A. Sq. Ft. per 1000 Sq. M.			29.0			32.7			36.0			38.0			28.2

	I.S.	L.A.	M.R.	W.C.	N.I.	Av.
<i>Corylus cornuta</i>		-				
<i>Acer spicatum</i>	x	x	x			
<i>Diervilla Lonicera</i>			.	x	x	-
<i>Symphoricarpos albus</i>			x	x	x	-
<i>Prunus virginiana</i>	.	-	.	.	x	.
<i>Lonicera canadensis</i>	-	.	.	.	x	.
<i>Taxus canadensis</i>	x	-	x	x	x	-
<i>Cornus rugosa</i>	x	x	x	-	x	-
<i>Rosa blanda</i>	x	-	x	x	x	-
<i>Lonicera hirsuta</i>		x	x	x	x	-
Space	90	79	78	82	46	75

FIG. 3. Shrub cover and frequency by stands. Length of bar indicates % of total shrub cover; width, frequency based on occurrence on transect segments 10 meters in length. See legend for Figure 2 for explanation of symbols.

	I.S.	L.A.	M.R.	W.C.	N.I.	Av.
<i>Cornus canadensis</i>					x	
<i>Aster macrophyllus</i>				.	x	
<i>Lycopodium clavatum</i>	.	.	-	-		
<i>Linnaea borealis</i>			.	.	.	
<i>Aralia nudicaulis</i>		.	.		.	
<i>Rubus pubescens</i>	.	.	.		x	-
<i>Clintonia borealis</i>	-	.			.	
<i>Maianthemum canadense</i>					.	
<i>Lycopodium obscurum</i>	.	.	.	x		-
Space	73	74	79	77	68	74

FIG. 4. Herb and pteridophyte cover and frequency. For explanation see legend for Figure 2.

	I.S.	L.A.	M.R.	W.C.	N.I.	Av.
<i>Calliergonella Schreberi</i>				.	.	
<i>Dicranum undulatum</i>	.	x		x	x	.
<i>Polytrichum spp.</i>	.	x	.	x	.	.
<i>Hypnum crista-castrensis</i> +		x	.	x	.	.
<i>Hylocomium splendens</i>	.	x	x	.	.	.
Space	31	67	38	70	82	58

FIG. 5. Moss cover and frequency. See Figure 2 for explanation.

most extensive fir-spruce-birch stands without a pine overstory. The tree canopy was relatively continuous. Fir was by far the most important in its contribution to cover and basal area (Fig. 2 and Table I). Black spruce occupied second place. The oldest fir showed 60 growth rings. Fir seedlings were abundant but saplings were few and occurred in the openings. Seedlings and saplings of other tree species were sparse.

The shrub cover was extremely low (Fig. 3). Shrubs were conspicuous only under openings in the canopy. Of the 52 herbs, including pteridophytes, only 5 contributed 1% or more cover (Fig. 4). Mosses were abundant, covering nearly three fourths of the forest floor (Fig. 5). About 10% of the area was covered with fallen logs in various stages of decay.

In terms of the total light striking the canopy,

the average light intensity based on 122 readings at 1 m. intervals along two 60 m. lines in the forest was 14%. This does not, however, indicate the great contrasts in light in the forest. The numbers of readings, per light intensity recorded, fall into two groups. One group (8% of the readings) were at or nearly 10,000 foot candles—or full sunlight. These readings represent the light in the openings in the forest. There were only scattered intermediate readings between these and 1000 foot candle readings, indicating the relatively sharp transition to the shade of the trees. Ninety-seven (80%) of the 122 readings were below 1000 foot candles (10% full light) which, according to Shirley (1945), is inadequate for survival of upland conifers of this region. (Shirley did not include the balsam fir in his study, but our observations would suggest that this intensity is too low for it also.) Sixty-five (53%) of the readings were below 500 foot candles (5% full light). When all readings exclusive of the openings (2000 foot candles and less) were averaged, the average amount of light penetrating the canopy was 4%.

Although there was evidence of former occupancy by pine, very few pines occurred in the stand. Only about 10% of the logs lying on the ground were identified as pine although some which were in late stages of decay beyond ready identification may have been pine. Pine stumps were evident at the west end of the stand. Since fir is more subject to breakage than to uprooting, the very uneven ground surface was also indicative of former pines which were destroyed during windstorms.

The central and eastern portions of the stand were mosaics. Dense growth of fir, open beneath, constituted a matrix in which there were small, partially open glades where shrub and herb growth were relatively luxuriant. In the western portion the fir was dense throughout, with an almost continuous carpet of moss on the ground.

The Lake Alice stand.—As with all of the stands, fir was the most important species in the Lake Alice stand. Its seedlings were common throughout, but saplings were few and limited to openings.

In the shrub layer the occurrence of *Taxus canadensis* (12% of the cover) was originally called to the authors' attention by Dr. D. B. Lawrence. It is noteworthy because the species is exceedingly rare in the Itasca Park area. Forty-one species of herbs not shown in Figure 4 were of minor importance in their contribution to cover. Mosses covered considerable of the forest floor,

and logs, over one half identifiable as pine, covered 9% of the ground.

This stand gave every appearance of having become established soon after a pine forest had been destroyed by fire. Abundant evidence of past severe fires in the form of charred stumps and logs suggested that the present forest was of relatively recent origin.

Stands of the Ely region

The Moose River stand.—This stand was the most impressive of the five stands and the most extensive of those studied in the Ely area. The forest canopy was very irregular. The fir averaging 40 ft. formed a rather dense and continuous layer. Spruces reaching heights of 75 ft. extended above the firs. Scattered large, old jack (*Pinus banksiana*) and white pines (*Pinus strobus*) towered above these to heights of 85 to 95 feet. Age determinations of jack pine, fir, black and white spruce revealed 2 of the jack pines, 17 and 18 inches in diameter, with 180 and 170 growth rings, and black and white spruce, 12 and 15 inches in diameter, with 105 and 125 growth rings. The largest firs were considerably younger—two trees 9 in. d.b.h. had 58 and 77 growth rings. Of especial significance was the large number of fir saplings and some spruce in the openings. No pine reproduction was recorded.

The shrub and herb layers were sparsely developed, but the moss layer was luxuriant. Not only did the mosses cover two thirds of the forest floor, but they almost completely covered the many large boulders and decaying logs.

Frequent windfalls formed tangles of felled trees. Many were uprooted while others, chiefly firs, were snapped off near the base. In these openings dense thickets of young fir predominated.

This stand gave the appearance of having been established through natural succession from a former pine forest. Many of the pines had fallen, but there were still a scattering of them towering above the spruces and firs.

The Wilderness Center stand.—The oldest fir whose age was determined showed 41 growth rings, while a white spruce had 95 growth rings with no evidence of a decrease in growth rate. Shrub, herb, and moss cover were low. Twenty-one species of herbs appeared in the quadrats, but only 3 contributed as much as 1% to the cover.

This area was formerly occupied by a pine forest. This was evident from the pine stumps left from lumbering operations, as well as from the uneven floor typical of an area where there have been wind-thrown pines.

Norway Island stand.—In this stand the fir had attained the greatest development, both in height and diameter, of all stands studied. The tallest balsam fir measured reached 70 feet. Trees 9.5 in. and 17 in. d.b.h had 52 and 60 rings.

The shrub layer was most continuous in this stand. Of 22 herbaceous species *Lycopodium clavatum* and *L. obscurum* contributed by far the greatest cover (Fig. 4). The moss layer was poorly developed (Fig. 5).

Soils

The soils in the Itasca Park stands were podzols. They were sandy throughout. The pH ranged from 5.1-5.3 in the A horizon and was 5.5 in the B horizon. In the Iron Springs stand limestone pebbles were found in the C horizon. There the pH was 6.1.

The soils of the stands in the Ely region were also podzols. They were generally very rocky and the ground in the Moose River stand was strewn with large boulders. The soils in general had a higher content of the finer-size particles (silt and clay) than those from the stands in the vicinity of Itasca Park. They ranged from pH of 4.0-4.7 in the A horizon to 4.5-4.8 in the B horizon.

Characteristics of the five stands

Three species of trees occurred in either the quadrats or on the transects in every stand. Of these three, balsam fir stood first in that it contributed a high percent of coverage in all stands, and an average of nearly three quarters of the cover for all stands (Tables I and II, Fig. 2). Although paper birch did not contribute nearly as high a cover, it was unquestionably second in this respect. White spruce could scarcely be con-

sidered a less important member of the community than paper birch even though it contributed less cover. Its strict form of growth in comparison with the spreading crown of *Betula* limited its contribution to cover, but its contribution to total basal area, 6.8% for all stands, was essentially the same as the 6.5% contributed by paper birch. No other species recorded equaled these three in importance except locally as conditions favored them in individual stands. There was only one tree which occurred in one area and not in the other. That was *Sorbus americana*, found only in the Ely region, while *Sorbus subvestita* occurred in both areas. The occurrence of *Sorbus* and its contribution to cover in both areas was very low, and there was little difference in the contribution the genus made in either place.

Reproduction was similar in pattern throughout the stands. The very high incidence of small seedlings of *Abies* throughout, especially on moss, was a pronounced feature; and the very low abundance of seedlings of other species was an equally pronounced feature. Saplings of any tree species were rare except in openings formed by a fallen tree or a group of trees. In such places there was generally found a vigorous growth of young firs.

Among shrubs, *Corylus cornuta* was prominent, being the only species having 100% constancy (occurring in sample plots of all stands). While some of the other species encountered were not uncommon in either region, they were either absent from the stand or so scattered that the sampling did not happen to record them. Two are of especial interest, *Taxus canadensis* and *Acer spicatum*. The former has been reported from only one other location in the immediate vicinity of Itasca Park. It is also known to occur in the vicinity of Ely but was not seen in any of the stands reported here. *Acer spicatum* is common in the maple-basswood forest at Itasca Park (Buell and Cantlon 1951) but did not show up in the sampling of the two upland fir-spruce-birch stands reported here. Nine species not included in Figure 3 show up in the data only once or twice and contribute an insignificant amount of cover. They are: *Alnus incana*, *A. crispa*, *Amelanchier stolonifera*, *Lonicera dioica*, *Rhamnus alnifolia*, *Rubus strigosus*, *Sambucus pubens*, *Vaccinium pensylvanicum* and *V. canadense*.

Of the 81 herbaceous species recorded for all five stands, only 8 had a constancy of 100%, or in other words, occurred in one or more of the quadrats of every stand (Fig. 4). Three of these, *Galium triflorum*, *Streptopus roseus* var. *longipes* and *Trientalis borealis*, contributed very little

TABLE II. Summary showing cover and basal area in all stands and constancy of tree species. Constancy here refers to occurrence in quadrats or on line transects in each stand. Smaller trees contributing an insignificant amount are omitted. They are *Amelanchier* spp., *Prunus pennsylvanica*, and *Sorbus* spp.

Species	Per cent average cover	Per cent average basal area	Constancy
<i>Abies balsamea</i>	72	69	100
<i>Picea glauca</i>	5	7	100
<i>Betula papyrifera</i>	12	7	100
<i>Picea mariana</i>	5	8	40
<i>Populus tremuloides</i>	2	3	60
<i>Pinus banksiana</i>	2	5	40
<i>P. resinosa</i>	<1	<1	40
<i>Fraxinus nigra</i>	<1	<1	40
<i>Populus grandidentata</i>	<1	<1	40
<i>P. balsamifera</i>	<1	<1	20

cover in any case and are not shown in Figure 4. Others not occurring with consistently high frequency could also be found in all the stands with further searching or sampling. This is true of *Cornus canadensis*, *Aster macrophyllus*, and *Rubus pubescens*, which did not occur in the quadrats at Norway Island, and of *Lycopodium obscurum*, which was absent from the quadrats at the Wilderness Center stand. These are mentioned especially since they were generally of primary importance in their contribution to cover in the herbaceous layer of the other fir-spruce-birch forests studied (Fig. 4). The herbaceous layer was rather open, covering an average of 26% of the ground and varying very little from this average in any one stand.

The moss layer in contrast covered an average of 42% of the ground for all stands but varied considerably from stand to stand (Fig. 5).

DISCUSSION

The fir-spruce-birch community in northern Minnesota, once it is established on upland sites, appears to be capable of reproducing itself. The fir is the only species whose seedlings are abundant; and when an opening occurs as the result of a blow-down, they grow rapidly, forming local thickets of young firs. Spruce seedlings do occur but not in abundance. As a tree, white spruce is present only as scattered individuals and its present reproduction does not indicate that it can be otherwise. Paper birch reproduces readily by stump sprouting, although seedlings are not uncommon, and young trees developing from seedlings are rare. These characteristics of the three principal species of the stands studied were also noticed by Cooper (1913) in his study of the climax forest of Isle Royale.

In the Itasca Park area the fir-spruce-birch forest appears to be able to displace other upland communities only on the moderately coarse soils, the maple-basswood community occupying the finer soils (Kell 1938). On the other hand, in the northeastern part of the state, at least in the region of Ely, there is evidence that this community can probably replace all others and reproduce itself on any but the most extreme habitats. Such soils as that underlying the Moose River stand, for example, probably would not be occupied by the conifers at Itasca Park, but by a maple-basswood community.

It is significant that all of the five stands included in this study were growing on sites recently occupied by pine forests. Kell showed that at the present time, natural succession on coarser soils in Itasca Park leads from pine forests to fir-

spruce-birch. Likewise pine forests in the Ely region commonly have considerable young fir and spruce in the understory, indicating that pine forests are today in the process of being replaced by the fir-spruce-birch community. The pine forests that occupied the sites used in this study had in most instances been destroyed by fire or by lumbering or by both. Only in the Moose River stand had the succession been apparently undisturbed. There, many of the large, old trees of jack pine and white pine were still standing, towering above the already well-established fir-spruce-birch forest. Although considerable search was made to find the fir-spruce-birch community where it had been occupying a site continuously, and people familiar with the forests of each area were consulted, no such stands were located.

The designation fir-spruce-birch has been used for this community in northern Minnesota, placing fir first because of its position of primary importance in all stands. It is outstanding in the per cent cover it contributes, the basal area, the numbers of individuals, and in its reproductive capacity. The white spruce is uniformly present in all stands but is superior to the fir only in its larger potential size and age. It is much inferior to fir in its reproductive capacity and probably will never be present as more than scattered individuals in these forests. A similar low reproductive capacity of the white spruce has been noticed in Canada (Candy 1938, Moss 1955). These fir-spruce-birch forests of Minnesota are ecologically very similar to the spruce-fir forests of New England and the mountains of western North Carolina.

Studies in the virgin spruce-fir forests of New Hampshire and the mountains of North Carolina (Oosting and Billings 1951) provide an interesting comparison with these conifer forests of Minnesota. Among species that are consistently present in the Minnesota stands, there are only a few that are also present in both the northern and the southern forests described by them.

None of the dominant tree species is consistently present in the three areas. Balsam fir and paper birch occur in the Minnesota and New Hampshire forests, but the Fraser fir (*Abies fraseri*) is the species Oosting and Billings found in the south. Yellow birch (*Betula lutea*) occurs in both the New Hampshire and North Carolina forests, but in Minnesota it was not found in the stands studied although it does occur occasionally in bogs in the Itasca Park region and in the Ely area. White spruce of the Minnesota forests is not represented in the New Hampshire forests studied, but its place is taken there by the red spruce (*Picea rubens*).

Acer spicatum is in both forest regions studied by Oosting and Billings and is important in the stands in the Ely region. Although it is common in some habitats in the Itasca region, particularly bogs, it is rare enough in the upland fir-spruce-birch stands not to have appeared in any of the sampling. The genus *Sorbus*, present as *S. subvestita* in the Itasca region and both *S. subvestita* and *S. americana* in northeastern Minnesota, is present as *S. americana* in both northern and southern forests in the east.

Among the herbs, *Clintonia borealis* is the one species that occurred in the quadrats of all of the Minnesota stands and also in all of the stands, both northern and southern, that Oosting and Billings studied. It was also present in a stand in northern Michigan studied by Jones and Zicker (1955). Three of the four herbaceous species that were uniformly present in the New Hampshire forests, though absent in the south, were among the most important ones in the Minnesota stands. These were *Cornus canadensis*, *Aralea nudicaulis* and *Maianthemum canadense*.

Among the mosses, *Calliergonella schreberi*, while by far the most important in Minnesota, is recorded from only two of the four stands in New Hampshire and is absent from the data of the southern stands. Some other species or group of species make up the well-developed bryophyte layer for at least two of the New Hampshire and all of the North Carolina forests. Oosting and Billings constructed cover diagrams for the northern and southern forests which show that in both, as in Minnesota, the bryophytes contribute considerable cover.

In general aspect the fir-spruce-birch forest of Minnesota and its counterparts in New Hampshire and North Carolina are very similar. Floristically they differ considerably, but in many instances there are corresponding species that may be considered ecological equivalents.

SUMMARY

1. In five relatively undisturbed upland conifer forest stands, two in the central part of northern Minnesota in the vicinity of Itasca State Park and three near Ely in the northeast, balsam fir, white spruce, and paper birch were consistently present among the dominant trees. Other trees were important only in certain stands or generally made only a minor contribution.

2. Among shrubs *Corylus cornuta* was the only species occurring in all stands.

3. Eight species of herbs occurred in the sampling of all five stands. *Cornus canadensis*, *Aster macrophyllus* and *Lycopodium clavatum* were most

important generally in their contribution to cover, but were absent from one stand. *Clintonia borealis* occurred not only in all five stands but also was reported by Oosting and Billings in all stands which they studied in New Hampshire and North Carolina.

4. In the well-developed moss layer, *Calliergonella schreberi* was the major contributor in all five stands.

5. All stands were on areas formerly occupied by pine. In most of them the pines had either been burned, cut or windthrown. In one the pines had been replaced through natural succession.

6. The fir-spruce-birch community gives every evidence of maintaining itself. Fir reproduction is the most successful and will continue to maintain for the fir a dominant role. Poor white spruce reproduction suggests that this species will continue to play a role secondary to fir. Paper birch wherever it gets established will persist by sprouting.

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SOME SAMPLING CHARACTERISTICS OF A SERIES OF AGGREGATED POPULATIONS¹

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Considerable interest has been shown recently in the spatial relationships of plant individuals and in methods for studying them (Cottam and Curtis 1949, Cain and Evans 1952, Goodall 1952, Clark and Evans 1954). The characteristics of a population of randomly dispersed individuals as shown by both fixed area samples and by distance measurements from exclusion angle methods have been described by Cottam, Curtis and Hale (1953). The theoretical mathematical basis of the observed characteristics has been provided by Morisita (1954). In a random population, the average distance from any individual to its nearest neighbor is equal to one half of the square root of the population mean area. The average distance from a random point to four individuals, each the closest to the point in a separate quadrant, is equal to the square root of the mean area. The average distance between an individual closest to a random point and its nearest neighbor outside of a specific angle of exclusion is an apparently linear function of the angle from 0° to 260°, with an angle of 100° giving a distance equal to the square root of the mean area. The most significant feature of all of these distances in a random population is their very great variability, thus necessitating a large sample if reasonable accuracy is to be obtained.

In the case of aggregated populations, the relationships between spacing distances and mean

areas are not so well known. Several investigators (Mueggler 1953, Clark and Evans 1954, and Morisita 1954) have suggested that such distances might be used as measures of aggregation, but they each proposed different sets of distances and different tests of significance. In view of these possibilities for assessing aggregation by the use of spatial measurements, it seemed desirable to investigate the behavior of interplant distances in populations of known degree of aggregation. The present paper presents a summary of these distances as measured by the same methods used in the earlier paper on a random population (Cottam, et al. 1953). Grateful acknowledgment is expressed to Miss Gwen Struik and Miss Donna Burr for their aid in collecting the data.

CHARACTERISTICS OF AGGREGATED POPULATIONS

An aggregated population is one in which the individuals are gathered into clumps or clusters of varying density and size. These clusters resemble the nodes of higher density usually present in a random population but are more extreme in character. A corollary of the tendency toward clumping is the presence of large areas which are free or nearly free of individuals in the spaces between the clumps. These also resemble the bare areas in a random population but are more extensive.

The clusters in aggregated populations may be represented by discrete clumps, as patches of *Corylus americana* in a pasture or tight colonies of *Antennaria neglecta* in a prairie, in which the leaves or branches of the individual plants are in contact with each other forming a closed canopy

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or leaf mosaic, with a constant density throughout the clump and no scattered or isolated plants between the clumps. The distance between individuals in such clumps is but a small fraction of the distance between clumps. Their outlines are clear and distinct and may be easily photographed or mapped. Such discrete clumps are common in nature and may be seen in a number of prairie and forest species. Typical species in Wisconsin communities are *Helianthus laetiflorus*, *Helianthus occidentalis*, *Coreopsis palmata*, *Solidago juncea*, and many bunch grasses in the prairie: *Aster macrophyllus*, *Maianthemum canadensis*, *Podophyllum peltatum*, and *Erythronium albidum* in hardwood forests, and many other species.

Other clusters are less dense, with interplant distances such that the individuals are not in contact but are slightly separated from each other. The clumps are nevertheless discrete and readily delimited, since there is no progressive increase in spacing toward the peripheries and since there are no isolated or scattered plants between the clumps. Such distributions are frequently seen in *Apocynum cannabinum*, *Asclepias syriaca*, *Asclepias verticillata*, many *Solidagos*, *Silphium integrifolium* and other species in the prairie, *Lonicera prolifera*, *Goodyera pubescens* and other common forest herbs, *Typha angustifolia* and the hybrids with *Typha latifolia*, *Pontederia cordata* and *Sparganium eurycarpum* in marshes, *Erigeron glabellus*, *Senecio pauperculus* and *Aster ciliolatus* in bracken-grassland and many other species too numerous to mention. Any ecologist who has worked in the field is familiar with a number of examples of this type of distribution. It should not be assumed, however, that all of the species listed above nor the other similar species always exist in this pattern of aggregation. Most of them may be found under conditions in which the clumps have become so large that the interclump distance approaches the interplant distance in magnitude. Usually there are scattered single plants, openings, or gaps within clumps and other irregularities when this stage is reached, and the recognition of individual clumps becomes difficult or meaningless. The fact that complicated distribution patterns do exist must eventually be taken into account by investigators of such matters, but their existence in no way detracts from the likewise frequent cases where discrete clumps are present.

Any consideration of aggregation must be closely tied to the questions of the areas involved, and to the homogeneity of that area. A species may have its individuals distributed at random when one size of area is considered, yet the same

individuals may be highly aggregated when another size of area is used. For example, the plants of *Quercus alba* within a single woodlot may be distributed at random but because woodlots are normally surrounded by cultivated fields, the woodlots themselves may be considered as aggregations of trees within a matrix of plowed land. The distribution of *Quercus alba* plants within a township or larger area is, therefore, one of extreme aggregation. The same situation also applies in less artificial situations. The clumps of *Erythronium albidum* may have the individuals distributed at random within the clumps, yet when the entire maple-basswood stand within which these clumps are found is considered, most of the forest floor is completely devoid of *Erythronium* plants, and the species must be considered to be highly aggregated. When the maple-basswood stand is considered together with the *Quercus* stands that may surround it and that contain no *Erythronium* plants at all, still another degree of aggregation is possible. Area, therefore, must be clearly defined before any statement of aggregation is meaningful.

Equally important is the necessity for homogeneity. A large field with a randomly dispersed population occupying only one portion of the area will appear aggregated by any test so far devised, if the entire area is sampled. Such cases of pseudo-aggregation are rather meaningless, since the unoccupied portion may have been totally unsuitable for the species involved. The plant under study should be found in all major subdivisions of the area studied; only under such conditions can its true propensities toward aggregation be found. The preceding discussion presupposes a constant type of aggregation within the area being studied. This is often not the case in natural communities. A species may be aggregated into tight clumps in one portion of an area and may undergo a transition from this highly aggregated condition to a stage in which the clumps get progressively larger until they anastomose, producing an almost solid stand with an occasional bare area as mentioned above. Further development of this type of system may eventually result in a situation in which the species is distributed at random. This lack of aggregation uniformity within a single study area is relatively common in nature, and the measurement of aggregation when such conditions occur is a problem of great complexity whose solution must await future developments. This paper does not attempt to deal with non-uniform aggregations, and the results presented herein should not be interpreted as being applicable to such situations.

Two major aims motivated this study. The first was to examine the basic variables present in aggregated populations. The second was to examine some of the indices that may be used to describe different degrees and kinds of aggregation. It was thought that these aims could best be achieved by restricting the study to relatively simple types of aggregation and limiting the variables to those that are related directly to aggregation. The populations studied were therefore constructed with equal numbers of individuals in equal areas. This limitation, while desirable in a study of this kind, should not be construed as a prerequisite for the application of the methods discussed to natural populations. The three indices of aggregation that will be treated in this paper were proposed by their authors as being applicable to natural populations, and have been used in the field. Two of them can be used without a knowledge of actual population density, and all three will provide a measure of the composite aggregation of the population regardless of how the aggregation pattern fluctuates within the population. The information on basic variables, however, is of more limited application. It requires that the population be homogeneous, be of known density, and possess discrete clumps that can be observed and measured. With these limitations, aggregation may be defined in terms of the number of clumps of the species and the proportion of the area which is occupied by clumps. The maximum degree of aggregation would be obtained when all of the individuals of the species were crowded together so closely that their stems made a single solid bundle, with decreasing aggregation being brought about by either increasing the number of clumps (and, in a population with a fixed density, decreasing the number of individuals per clump) or increasing the distance between individuals within the clump (which would automatically increase the area occupied by the clumps).

With homogeneous populations of a uniform aggregation pattern having a known density and a known area, we propose that aggregation may be adequately described in terms of three inter-related variables, any two of which will determine the third. These variables are: 1. The clump mean area (K). This is the area of the population divided by the number of clumps. 2. Area of clumps (C). This is the average area that would be obtained if a planimeter were drawn around the perimeter of each clump. 3. The within-clump mean area (W). This is the area of each clump divided by the number of individuals it contains. These variables are shown plotted against each other in Figure 1. The figure has been constructed

with all three axes on a logarithmic base for two reasons. The first is that it permits the placement of a wide range of possibilities on the same figure. The second is that it is the only base on which successive values for each variable are parallel. We believe that any degree or intensity of simple aggregation can be defined by these three variables, and we propose to show that the existing methods of assessing degree of aggregation actually are based on these three parameters.

Figure 1 gives these variables in terms of the area of the population (A) and the number of individuals the population contains (N). The values in parentheses are based on the parameters in square millimeters of the populations used in the present study. Any aggregated population will have a locus on this figure, but the actual values for A and N will determine the numerical values for each K , C , and W . Values for K , the mean area of the clumps increase toward the left. They approach a lower limit of A/N on the right side, since there can be no more clumps than there are individuals in the population. Actually, the right side of the figure is an asymptote that can never be reached with an aggregated population. A/N is an expression of population mean area (PMA). When K equals PMA, the population has no clumps and is either random or regular. The maximum value for K is reached when all the individuals of the population are grouped into a single clump, at which time K equals A . In actual practice a one-clump population is not measurable for purposes of determining degree of aggregation, since between-clump distances cannot be obtained for such a population.

The values for C , clump area, approach but do not reach A , at the apex of the figure. When this point is reached, there can be only one clump, and it must have an area equal to the population area. This is also a random or regular distribution. The minimum value for C approaches zero at the bottom right side of the figure, where all the individuals of each clump occupy a dimensionless point.

W , the within clump mean area, is limited at the top of the figure by A/N . Under these conditions, the area occupied by a single individual within a clump would equal the population mean area, and the condition of randomness or regularity would again prevail. The lower limit for W approaches zero, as with C above.

An understanding of some of the relationships of these three factors can be gained through an examination of the figure. C cannot be larger than K but can be any value less than K . W cannot be larger than A/N , and is further limited to

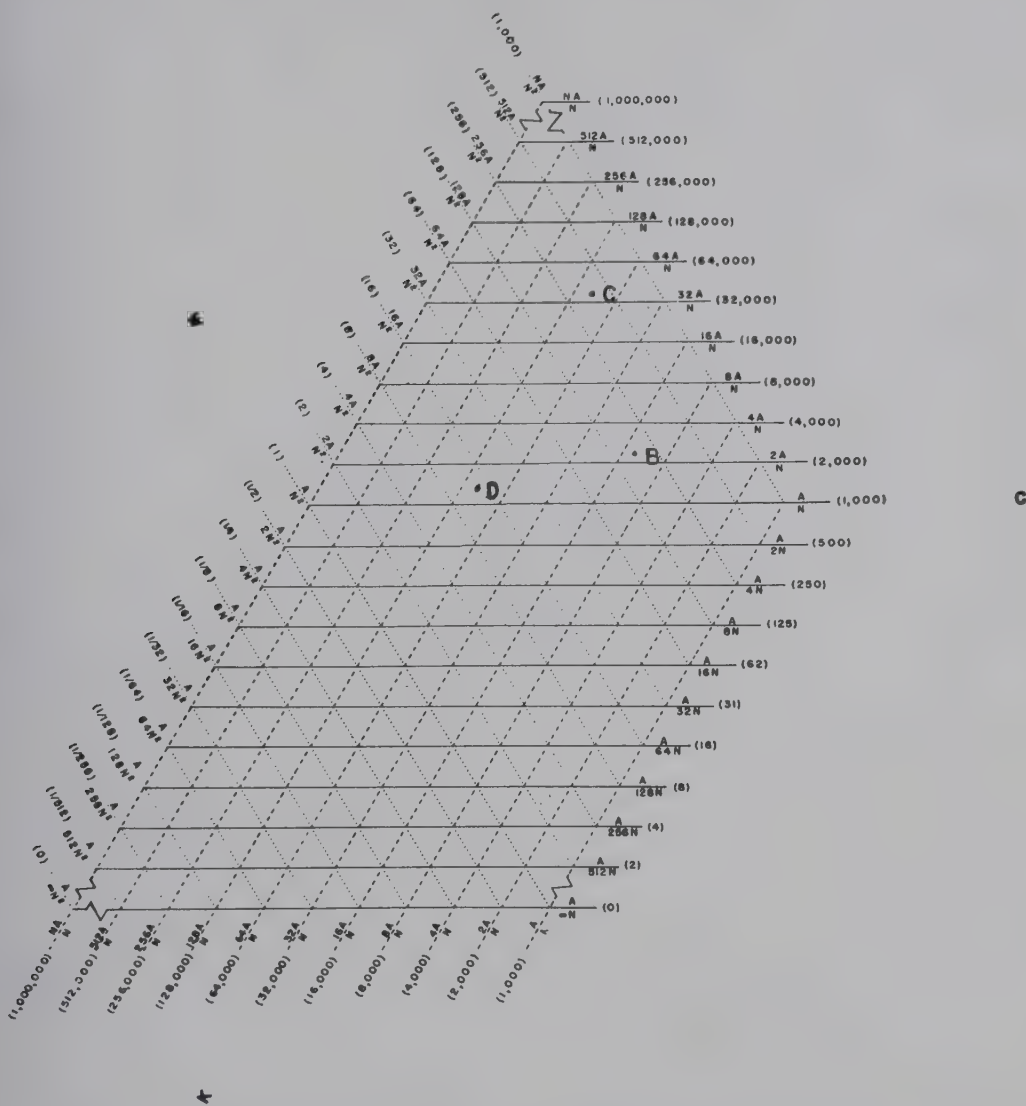


FIG. 1. The relationships of three factors used to describe degree of aggregation. Values for the three factors are given in terms of the population parameters: population area (A) and population density (N). K (dashed lines) is mean area of the clumps. C (solid lines) is the average area of a clump. W (dotted lines) is within-clump mean area. The three points located in the body of the figure are the loci for the three aggregated populations used in this study. Actual values of the three factors are given in parentheses along the margins of the figure.

a value less than that of C. The minimum value of W is C/N , and this value is reached only when K equals A; that is, when the population consists of a single clump.

Maximum aggregation is achieved when the area of the clumps (C) is small and K, mean area of the clumps, is large. Thus, the locus of maximum aggregation is the lower left angle of the

figure. Minimum aggregation is found just inside the two right hand edges of the figure. Within the body of the figure, aggregation generally increases from right to left. The same degree of aggregation may be achieved through a variety of combinations of K, C, and W values. A combination of a small K value with small C and W values will result in moderate aggregation, as will a com-

bination of a large K value with large C and W values, etc.

MEASUREMENT OF DEGREE OF AGGREGATION

A variety of methods have been proposed which will determine whether or not a particular population is random (discussed in Goodall 1952). Practically all of these methods are dependent in one way or another upon the fact that a random dispersion may be described by a Poisson distribution. Provided that the mean density of a population is known, various other characteristics of the population may be calculated through the use of the Poisson formula. Thereafter, a comparison of the observed level of these characteristics with the theoretical value will indicate whether or not the population was indeed random.

While such an indication is of great value, it would be more useful if a measure of the degree of departure from randomness could be obtained. The ultimated refinement would be a measure that would allow observed values to be adjusted to produce true density values, with consequent increase in their phytosociologic usefulness. Unfortunately, most of the methods utilizing the Poisson relation are based upon the results obtained with area samples and hence are greatly influenced by the size of the quadrat or other sample used to obtain them (Curtis and McIntosh 1950, Evans 1952, Thompson 1952).

It has been suggested by Goodall (1952), Mueggler (1953), Hopkins (1954), Clark and Evans (1954), Morisita (1954), and Catana (1954) that a point sampling method, utilizing distances between individuals, might be a better approach to the problem and might have greater chance of providing a direct measure of the amount of aggregation. Mueggler, Hopkins, Clark and Evans, and Catana each proposed an index of aggregation based on distance measures. Mueggler (1953) and Catana (1954) proposed that the ratio of the interplant distances between pairs of individuals separated by two different angles of exclusion be used as the measure. Clark and Evans (1954) indicated that a comparison of observed and expected distances between each individual and its nearest neighbor would provide the necessary measure. Hopkins utilized the nearest neighbor distance of Clark and Evans and a distance corresponding to the Q_1 of Cottam and Curtis (1956) but his index is based on the ratio of sums of squares rather than means.

For the sake of convenience, these measures have been given letter designations, which will be used throughout the remainder of the paper. These designations and their relationships with random and aggregated populations are given in Table I.

The indices used by Mueggler and Catana are

TABLE I. List of symbols, their meanings and relationships, used in this paper

Designation	Description	Relationships with random populations	Relationships with aggregated populations
Y	Measure of within-clump distance.		
Y_r	Mean of distances measured from randomly selected individuals to their nearest neighbor.	$0.5 \sqrt{PMA}$	$0.5 \sqrt{W}$
Y_n	Mean of distances measured from individuals closest to randomly selected sampling points to their nearest neighbor. This is the random pairs distance using a zero degree angle of exclusion.	$0.6 \sqrt{PMA}$	$0.6 \sqrt{W}$
X	Measure of between-clump distance.		
X_{100}	Random pairs distance using 100° angle of exclusion.	$\sqrt{PMA}$	$\sqrt{K} - \sqrt{1.27 C}$
X_{180}	Random pairs distance using 180° angle of exclusion.	$\sqrt{PMA} \times 1.25$	$(\sqrt{K} - \sqrt{1.27 C}) \times 1.25$
Q_m	Mean of values using the quarter method.	$\sqrt{PMA}$	$\sqrt{K} - \sqrt{1.27 C}$
Q_1	Distance from a randomly selected sampling point to the individual closest to the point. The shortest of the four quarter values.	$0.5 \sqrt{PMA}$	$0.5 (\sqrt{K} - \sqrt{1.27 C})$
X_c	Any of the above X values corrected to equal Q_m or X_{100} .	$\sqrt{PMA}$	$\sqrt{K} - \sqrt{1.27 C}$

very similar. Both these workers set up a ratio of the average distance between clump perimeters (X) and the average within-clump distance. The latter is measured by Y_n . Mueggler used X_{180}/Y_n as his ratio. For random populations this is equivalent to $1.25 \sqrt{PMA}/0.6 \sqrt{PMA}$, or 2.08. Catana used X_c divided by $5/6 Y_n$. His theoretical value for a random population is 2.00. In the following discussion, these two indices will be considered to be identical, and will be called the Mueggler-Catana index. Their index increases as the distance between clump peripheries increases, Y remaining constant, or increases as distance between individuals within clumps decreases, X remaining constant. With a population containing a fixed number of individuals in a fixed area, an increase in the X value can be obtained by decreasing the area of the clumps, or by decreasing the number of clumps, either of which will result in an increased distance between clump peripheries. The Y value can be decreased only by decreasing the within-clump mean area. The values of this index vary from one, for an absolutely regular population to infinitely large values for populations exhibiting extreme aggregation.

The method of Clark and Evans makes use of a nearest neighbor value (Y_r) that differs from the Y_n value discussed above in the details of selection of the individuals between which nearest neighbor distances are measured and has a slightly lower value. Their index is the ratio of the expected Y_r value divided by the observed Y_r value. Expected Y_r value is computed from the known density of the population. The values of this index vary from zero for a condition of extreme aggregation to 2.1491 for a perfectly regular hexagonal distribution.

Hopkins proposed a ratio obtained by dividing sums of the squares of the distances from randomly selected sampling points to the nearest plant individual (Q_1) by the sums of squares of the Y_r values discussed above. His index ranges around the value one, with values less than unity indicating regularity and values greater than unity indicating aggregation.

METHODS

It is easily possible to locate on Figure 1 several populations which differ in the three major variables. Three such populations are located. Maps were made of artificial populations which corresponded to the loci indicated. These were constructed using a fixed population of 1,000 individuals in a fixed area of 1,000,000 sq. mm. in each case. The proper number of clump centers was laid out with the use of coordinates from a ran-

dom numbers table. A circle of proper diameter was located around each point and the required portion of the total population was placed at random within each circle. The placement of the individuals was greatly facilitated by the use of a special random numbers table prepared through the courtesy of Mr. Fred Gurenberger of the University of Wisconsin Numerical Analysis Laboratory. This table of square coordinates was specially marked so that all of those loci which fell outside of an inscribed circle of diameter equal to the side of the square were eliminated. The resulting populations thus had a constant number of individuals in a constant total area located at random in clumps which were dispersed at random throughout the area. They differed from each other in size and number of clumps and in number of individuals per clump. Population B had many small clumps with few individuals per clump while populations C and D had few clumps with many individuals per clump but differed in the size of the clumps, with D having approximately the same clump size as B, but with C having much larger clumps. Population A had all individuals at random.

A uniform border containing half the total population area was delimited around the edges of each population. All sampling points were laid out in the remaining portion of the population by a stratified random system, although distances were measured to individuals within the border area if the sample called for it. The border was used to minimize edge effects, and its large size was necessary because of the extreme aggregation of some of the populations.

The parameters of the four populations are given in Table II. The central portions of each population are shown in Figures 2 through 5 to give a visual impression of the variation in aggregation.

Each population was sampled with 200 quadrats

TABLE II. Parameters of four artificial populations. All distance measurements are in millimeters

Parameter	POPULATION			
	A	B	C	D
Total area—A.....	500,000	500,000	500,000	500,000
Total number of individuals—N.....	499	495	591	540
Pop. mean area—PMA.....	1,002.04	1,010.1	846.0	925.9
Number of clumps.....		36.79	5.91	5.39
Mean area of clumps—K.....		13,592.2	84,602.4	92,764.4
Number of individuals per clump.....		13.46	100.0	100.18
Area of clumps—C.....		2,431.8	35,076.5	1,379.5
Mean area within clumps—W.....		180.67	350.77	13.77

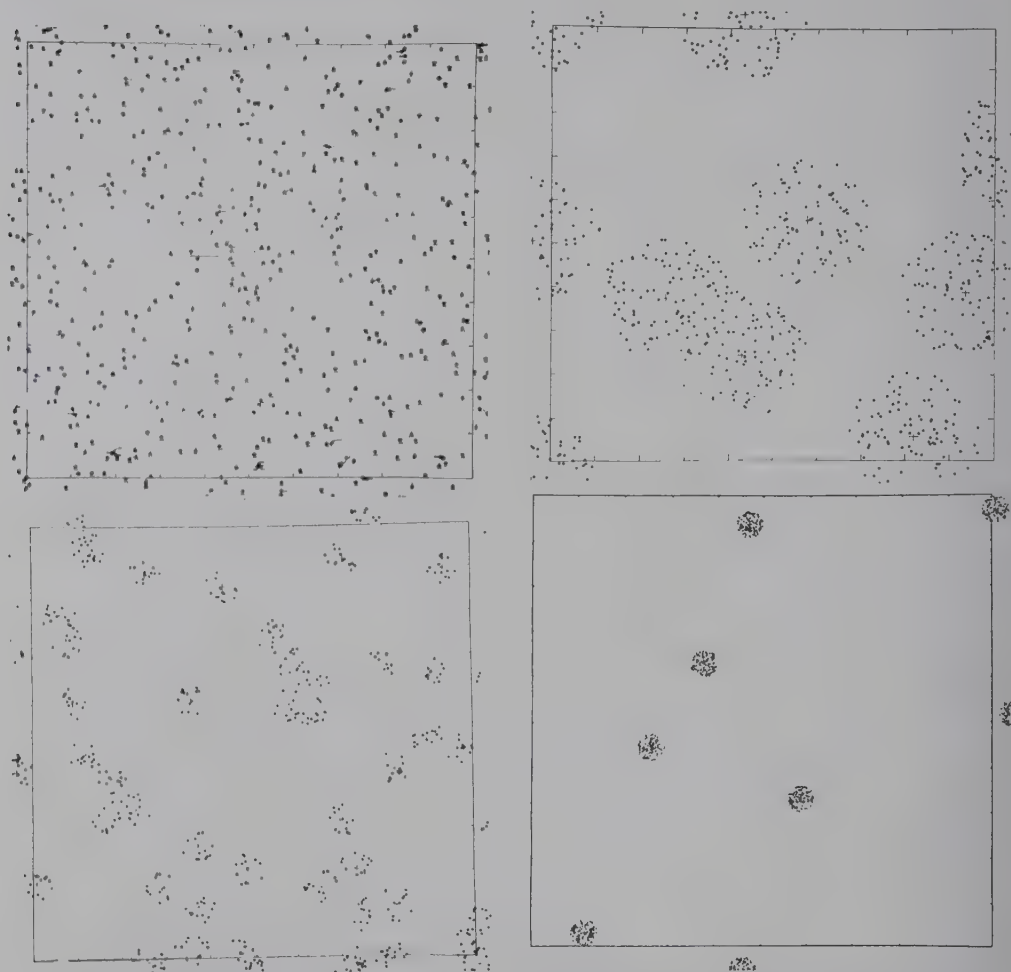


FIG. 2-5. Reproductions of the center portions of the populations used in this study. Figure 2 is population A, 3 is population B, 4 is population C, 5 is population D. For the parameters of these populations, see Table 2.

(equal in size to two times the population mean area) centered on each sampling point, with 200 points for the point centered quarter method, and with 200 random pairs using 0° , 100° , and 180° angles of exclusions at each sampling point. The same sampling points were used for each method. The zero degree angle in effect gives a measure of the nearest neighbor distance (Y_n). The shortest distance (Q_1) of the quarter method is the closest individual distance of Hopkins, and the two larger angles of the random pairs method provide different estimates of the distance between clump perimeters.

RESULTS

The quadrats gave results in accord with ex-

pectation for all four populations. These are summarized in Table III. Populations B, C, and D differ markedly from population A in all measurements except for density per quadrat. Populations B and C, however, are very similar in their characters in spite of the fact that their parameters differ in several important ways. The D/d measure of aggregation of McGinnies (Curtis and McIntosh 1950) shows this similarity very well.

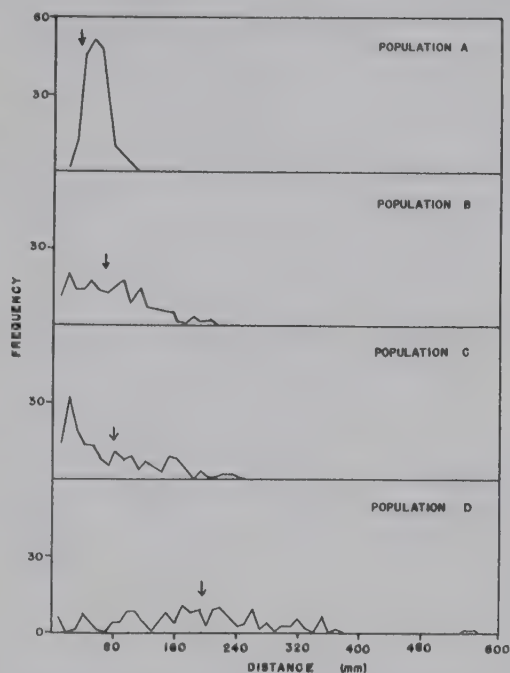
The quarter data are summarized in Table IV. The very high coefficients of variation shown by the distance measurements reflect the fact that the closest one or two individuals might be in the same clump while the others are in one or possibly in two different clumps. Since the sampling point

TABLE III. Summary of quadrat results, using 200 quadrats each twice the population mean area in size

Measurement	POPULATION			
	A	B	C	D
Frequency.....	88%	46%	44%	7%
Density per quadrat.....	2.01	2.66	1.85	2.59
Ratio, actual density to expected density (D/d)....	0.94	4.29	3.19	37.00
Variance/mean.....	0.81	5.84	3.32	50.33
Probability from Chi squared for Poisson distribution....	0.50	.01	.01	

TABLE IV. Summary of quarter results, using 200 samples at the same set of sampling points used for quadrats

Measurement	POPULATION			
	A	B	C	D
Average distance from point to the 4 individuals (Q_M).....	32.05mm	64.83mm	79.19mm	195.15mm
Standard deviation.....	7.6	45.7	75.6	106.7
Coefficient of variation.....	23.7%	70.6%	95.6%	54.6%
Variance/mean.....	1.8	32.0	72.3	58.3
Q_1	16.19	35.18	42.87	101.18
Q_2 as % of Q_1	160.7%	142.9%	135.5%	157.0%
Q_3 as % of Q_1	221.9%	197.0%	183.2%	222.0%
Q_4 as % of Q_1	309.5%	298.6%	334.7%	317.6%
$Q_M/\sqrt{PMA}$	1.01	2.04	2.72	6.42

FIG. 6. Frequency polygons of the Q_m distances obtained from the four populations. Arrows indicate mean distance.

by chance might be located within or immediately adjacent to a clump in one case or might be a considerable distance from it in another case, the inherent variability is very great.

In spite of the great differences in degree of aggregation in the four populations, the relationship between the four separate distances from the point to the individuals in each separate 90° quadrant when ranked in order from the shortest (Q_1) to the longest (Q_4) is remarkably constant, with the Q_2 distance being about $1\frac{1}{2}$ times the Q_1 distance, the Q_3 2 times, and the Q_4 3 times. The data reflect the degree of aggregation by an increase in distance with increasing deviation from randomness. The average distance from the point to all four individuals on each set (Q_M) is almost exactly equal to $\sqrt{PMA}$ for population A, but is over 6 times as great for the most aggregated population D (Table IV).

Frequency distribution polygons of the combined distances to individuals in all four quadrants for each population are shown in Figure 6.

The angle of exclusion methods, using the distance between the individual nearest the point and a second individual separated from the first by a given angle, were studied in detail because of their potentiality for providing direct information on

distances within clumps and between clumps. The data for three different angles are summarized in Table V. As was the case with the other methods, populations B and C are quite similar to each other in most of their measured characters but both are very different from population D. The greater coefficients of variation in population C are related to the fact that a relatively large percentage of the sampling points fell within the clumps because of the large size of the clumps. This situation occurred least frequently in population D and the variation in this case is more like that in the random population A. The ratio *variance to mean* (V/M) is not proportional to the degree of aggregation at any angle of exclusion. It appears to be most dependent upon the percentage of points falling within the clumps, but the relationship is curvilinear and irregular.

The average distance between the individuals is a function of the angle of exclusion, but the exact relationship is dependent upon the degree of aggregation. This is shown in Figure 7, where the distance is expressed as a percentage of the $\sqrt{PMA}$ for each angle and each population. The relationship appears to be linear for the random population, as was shown by Cottam et al. (1953), but becomes increasingly curvilinear as aggrega-

TABLE V. Summary of distances by the random pairs method using different angles of exclusion

Measurement	POPULATION			
	A	B	C	D
0° angle of exclusion:				
Average distance.....	18.85mm	9.09mm	12.18mm	2.59mm
Variance/mean.....	4.23	2.19	4.42	0.51
Coefficient of variation.....	47.4%	51.3%	60.2%	44.5%
Av. distance/ $\sqrt{\text{PMA}}$	0.59	0.29	0.42	0.85
% of pairs which were within the same clump.....		100%	100%	100%
100° angle of exclusion:				
Average distance.....	31.42mm	62.27mm	73.05mm	236.59mm
Variance/mean.....	3.70	27.28	56.97	21.53
Coefficient of variation.....	34.3%	66.2%	88.3%	30.1%
Av. distance/ $\sqrt{\text{PMA}}$	0.99	1.95	2.50	7.77
% of pairs which were within the same clump.....		35.0%	69.5%	3%
180° angle of exclusion:				
Average distance.....	40.77mm	90.95mm	103.9 mm	272.70mm
Variance/mean.....	5.09	25.22	62.42	20.88
Coefficient of variation.....	35.3%	52.9%	76.7%	27.6%
Av. distance/ $\sqrt{\text{PMA}}$	1.29	2.85	3.57	8.96
% of pairs which were within the same clump.....		19.0%	40.5%	2%

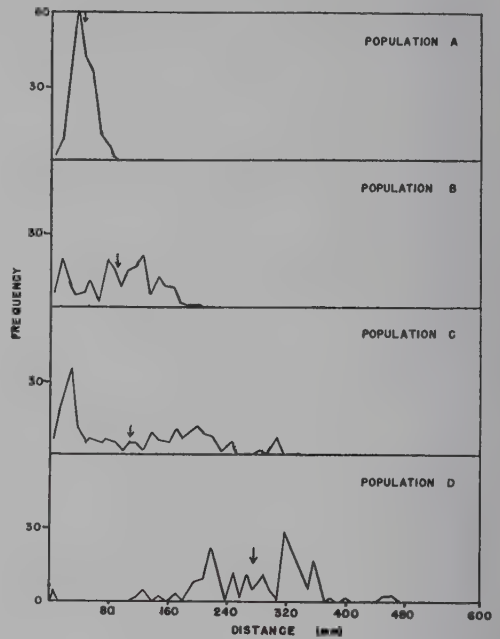


FIG. 8. Frequency polygons of distances obtained using the random pairs method with 180° angle of exclusion. Arrows indicate mean distance.

DISCUSSION

The extreme degree of variation present in the interplant spacing distances in a randomly dispersed population has been pointed out earlier (Cottam, et al., 1953). In the aggregated populations of the current study, this variation is greatly accentuated. The variance/mean ratios reach such tremendous levels as 72.3 (population C, Table IV) while the coefficient of variation attains a value of 95.6% in the same case.

Some population characteristics remain relatively constant, regardless of the degree of aggregation. This is especially noticeable in the case of the ratios between the four separate distances in the quarter method, and in the density values for the quadrat method.

Populations B and C differ considerably in their parameters with many small, tight clumps in population B and few, large diffuse clumps in population C. In spite of this, they show similar indices of aggregation by all methods used. This results from the fact that the ratio of within-clump spacing to between clump spacing is about equal in the two cases and indicates that the same degree of aggregation may be brought about by different combinations of clump sizes and spacings. Both of these populations differ markedly from popula-

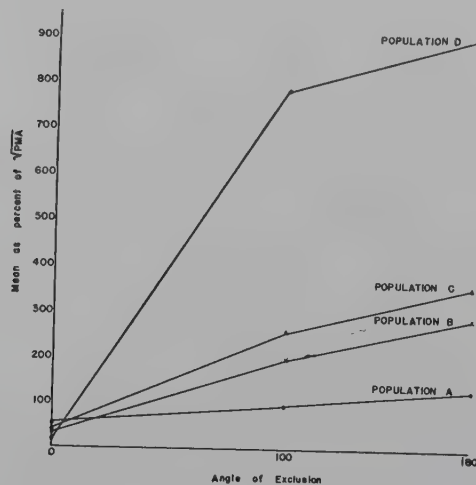


FIG. 7. Effect of angle of exclusion on distances obtained using the random pairs method.

tion D in most of their characteristics and have very different indices of aggregation.

With all the aggregation indices, one of the distances used is a measure of within-clump distance, and is either Y_r or Y_n . Theoretically, Y_r is the more appropriate measure, but its determination requires the random selection of individuals in the population. As discussed elsewhere (Cottam and Curtis 1956), this is difficult to do in the field. The Clark and Evans method of numbering all plants in the population and extracting a random sample by means of a random numbers table requires the counting and tagging of all individuals in the population, an impossible task with many natural populations. Their alternative suggestion of laying down quadrats at random and measuring all nearest neighbor distances within each quadrat is also apt to be very time consuming with highly aggregated populations. Hopkins used the approximation of selecting every fifth plant and measuring the distance from this plant to its nearest neighbor. This method is neither random nor completely objective. The measure Y_n , which is based on the selection of individuals by means of their proximity to randomly selected sampling points, has the advantages of objectivity and efficiency, and the disadvantage that its value was arrived at empirically rather than theoretically.

The indices all compare this within-clump measure with another measure, variously arrived at. Clark and Evans compare Y_r with the expected Y_r that would be obtained had the individuals in the population been distributed at random. This index requires a knowledge of true population density. Hopkins compares Y_r with the value for Q_1 . These two measures have identical values and identical variances in a random population (Morisita 1954) and the ratio of the two will be unity for such a population, regardless of whether means or sums of squares are used. With aggregated populations, Q_1 becomes a measure of distance between clump perimeters and increases rapidly, while Y_r decreases.

The X/Y_n index of Mueggler and Catana also compares within-clump distances with between-clump distances. Here a variety of alternatives exists for determination of between-clump distance. X_{100} can be used directly, since its value equals $\sqrt{PMA}$ for random populations. X_{180} must be divided by 1.25 (or multiplied by 0.80) to yield the same value. Q_m equals $\sqrt{PMA}$. $Q_1 \times 2$ also equals $\sqrt{PMA}$. Any of these values can therefore be corrected to equal one another. The results of this correction are shown in the first four rows of Table VI. Results for popula-

tion A, the random population, are in very close agreement, with greater variation occurring in the aggregated populations. In only one case does the figure for any value differ from the mean of all four by more than ten per cent, and this is the X_{100} value for the most highly aggregated population, population D. In view of the highly variable results normally obtained with aggregated populations, this degree of agreement is considered to be satisfactory. The between-clump measures yield the distance between clump perimeters.

TABLE VI. X_c values obtained through the use of different methods. Explanation in the text

Method	POPULATION			
	A	B	C	D
$X_{180} \times 0.80$	32.62	72.76	83.12	218.16
X_{100}	31.42	62.27	73.05	236.59
Q_m	32.05	64.83	79.19	195.15
$Q_1 \times 2$	32.38	70.36	85.14	202.36
$\sqrt{K} - \sqrt{1.27 C}$ from Population Parameters		62.07	79.83	262.7

Since they measure either the distance from a sampling point to the closest individuals to that point, or the distance from an individual closest to a sampling point to the individual closest to it outside an exclusion angle, they usually measure distances to individuals on the perimeters of clumps. Had measurements been made to clump centers rather than clump perimeters, these distances would equal, or could be corrected to equal, $\sqrt{K}$, since the clumps are distributed at random and the clump centers constitute a random population, the mean area of which is K . Measurements were made to clump perimeters rather than clump centers, so the X distances described above should estimate the population parameter $\sqrt{K} - \sqrt{C}$, or the distances between clump centers minus the diameters of the clumps. A more accurate representation of clump diameter is $\sqrt{4C/\pi}$, or $\sqrt{1.27 C}$, since the clumps are circular rather than square.

The data in Table VI show that results for populations B and C provide reasonable approximations of $\sqrt{K} - \sqrt{1.27 C}$, but that the values for population D are consistently low. Part of this decrease in values may be due to the number of X distances measured from points which fell within clumps, but this is not the complete answer. Even when these "within-clump" X distances are excluded, and the mean X distance is computed from those distances that were measured from sampling

points located between clumps, the value is not as large as it should be. A possible answer lies in the fact that populations C and D have only ten clumps, including the border area, a number too small to be used as an accurate basis for determining distances. Larger numbers of clumps were not used because of physical limitations. The size of the clumps could not be decreased without having the individuals within clumps so close together that their placement would be in error. The size of the map could not be increased without making it so large that it would have been exceedingly difficult to work with.

An index containing factors for both the between-clump and within-clump components of an aggregated population is $\frac{\sqrt{K} - \sqrt{1.27 C}}{\sqrt{W}}$. In this

index, the numerator is the between-clump distance, which increases as aggregation increases, other factors remaining constant. The denominator is the within-clump distance, and as this distance gets smaller, aggregation also increases. Thus, the index gives higher values with increasing aggregation whether this increase is brought about by increasing the distance between clumps, decreasing the distance within clumps, or both. The theoretical end-point of this index is infinity for highly aggregated populations. The value for minimum aggregation approaches zero as K and C become equal, and W approaches A/N. $X_c/2Y_r$ provides a close approximation to this index for moderately aggregated and highly aggregated populations. When populations with only a slight degree of aggregation are measured, X_c becomes a measure of $\sqrt{PMA}$, and $2Y_r$ is also a measure of $\sqrt{PMA}$. Thus $X_c/2Y_r$ has a lower limit of one rather than zero.

The three indices used in this investigation are all based on the same general principle—the relationship between the nearest neighbor distance and some other measured or computed distance which bears a known relationship to the nearest neighbor distance in random populations.

In the notation of Figure 1, the indices may be written as follows:

$$\text{Clark and Evans } \frac{1/2 \sqrt{W}}{1/2 \sqrt{PMA}} \text{ or } \frac{\sqrt{W}}{\sqrt{PMA}}$$

$$\text{Mueggler and Catana } \frac{\sqrt{K} - \sqrt{1.27 C}}{1/2 \sqrt{W}}$$

Since Hopkins used sums of squares of individual measurements rather than the means of these same measurements, his index cannot be written in the above notation. His index is

$\epsilon Q_1^2 / \epsilon Y_r^2$. Had he used the means of these values rather than sums of squares, his index would read, in the above notation,

$$\frac{1/2 (\sqrt{K} - \sqrt{1.27 C})}{1/2 \sqrt{W}} \text{ or } \frac{\sqrt{K} - \sqrt{1.27 C}}{\sqrt{W}}$$

Table VII presents a comparison of the indices.

TABLE VII. Comparison of indices of aggregation used by various authors

Investigators	POPULATION			
	A	B	C	D
Clark and Evans.....	0.96	0.46	0.62	0.13
Hopkins.....	1.03	26.38	28.78	2,114.62
Mueggler-Catana.....	2.04	8.56	7.80	90.34
R Qm R 5/6 YnR				
D/d.....	0.94	4.29	3.19	37.00
Transformed Values				
Clark and Evans.....	1.04	2.17	1.61	7.69
Hopkins.....	1.01	5.03	5.36	45.98
Mueggler-Catana.....	1.02	4.28	3.90	45.17
D/d.....	0.94	4.29	3.19	37.00
$\sqrt{K} - \sqrt{1.27 C}$		4.62	4.26	70.80
$\sqrt{W}$				

The first part of the table gives the indices as they were used by the various authors. The second part attempts to put them on a more nearly equal numerical basis by adjusting the figures to make them as closely equivalent to

$$\frac{\sqrt{K} - \sqrt{1.27 C}}{\sqrt{W}}$$

as possible. The reciprocal of the Clark and Evans index has been used, since they have $\sqrt{W}$ in the numerator rather than the denominator. The Clark and Evans index has no term for between-clump distances, and uses instead $\sqrt{PMA}$. With populations of fixed density such as those used here, this value is a constant. Their index will therefore vary only as within-clump distance varies, and will show smaller changes with changing aggregation than the other two, which include a term for between-clump distance as well as within-clump distance.

The Hopkins index is very similar to the Mueggler-Catana index except that sums of squares have been used. The square root of this index provides only a rough approximation of $\frac{\sqrt{K} - \sqrt{1.27 C}}{\sqrt{W}}$, but the results, as seen in Table

VII are fairly close to the adjusted Mueggler-Catana index. The Mueggler-Catana index has been halved.

It should be emphasized that although the above

transformations yield figures of the same order of magnitude, they would not be expected to be identical, since the indices either require different, though related, values for their determination or are based on different treatments of the same values. The fact that they can be changed by simple transformations to yield nearly equal values over a wide range of types of aggregation is an indication that they are all measuring the same characteristics of the populations.

From the above discussion, it appears that the measurement of aggregation by means of distance methods may be accomplished with a variety of indices. The indices discussed in this paper are closely related, and all of them may be interpreted in terms of one or more of the factors plotted in Figure 1. Each of the indices estimates $\sqrt{W}$. With the Clark and Evans index, $\sqrt{W}$ is the only variable when populations of equal density are measured. The Hopkins and the Mueggler-Catana indices estimate in addition the term $\sqrt{K} - \sqrt{1.27 C}$. Neither method provides a measure that can be used to determine the value of either $\sqrt{K}$ or $\sqrt{C}$. They provide only a measure of the difference between them.

Perhaps the most important result of this investigation is the demonstration that aggregation may indeed be defined in terms of three factors, mean area of Clumps (K), mean area within-clumps (W), and area of clumps (C). The factors are interrelated. When populations of known density per unit area are used, a knowledge of any two will permit determination of the third. When populations of unknown densities are used, additional measurements are required to determine K and C . W can be measured as described above. C can be determined by direct measurement of clump diameters in populations with well defined clumps, or can be estimated by the Wandering Quarter method of Catana (1955). The measurement of clump diameters, even when the clumps are well defined, is not as simple as it appears since the area dominated by a single plant within a clump extends in all directions from the stem as far as the roots extend, or the tops cast shade. As an arbitrary standard procedure, this laboratory considers the clump perimeters to be located at a distance equal to one half $\sqrt{W}$ beyond the central stem of the outermost plants in the clump. Knowing C , K may be determined by substitution in the equation $X_c = \sqrt{K} - \sqrt{1.27 C}$. Knowledge of these three factors is essential for an adequate description of a simple aggregated population. Indices such as the ones described in this

paper do not provide an adequate description because the degree of aggregation measured by the indices may be arrived at by various combinations of the three factors, and several populations differing widely in their parameters will have the same index. This is no fault of the index. It is merely a statement that the same degree of aggregation may be obtained in several different ways.

It should be re-emphasized that the populations used in this study were exceedingly simple in comparison with many natural plant populations. This simplicity was essential for the study of the basic variables affecting aggregation. The fact that most natural populations are more complex in no way indicates that the variables concerned are different. Rather, these complex populations are a continuum of varying aggregation patterns, any small segment of which is capable of being described in terms of the material presented in this study. The indices described yield a measure of over-all aggregation regardless of the differences present in the population, but as is the case with all averages, these indices become less meaningful as the population being measured becomes more variable.

SUMMARY

Aggregation may be defined in terms of three variables: the clump mean area (K), the area of the clumps (C), and the within-clump mean area (W). These variables have been plotted in Figure 1. With populations of known density and known area, knowledge of any two of these variables will permit determination of the third. Other factors remaining constant, aggregation increases as the area of the clumps decreases, as the within-clump mean area decreases, or as the clump mean area increases.

Three indices for the measurement of aggregation using distance methods are discussed. It is shown that these indices compare a measure of nearest neighbor distance (which in aggregated populations is a measure of within-clump mean area) and some other measured or computed distance which bears a known relationship to the nearest neighbor distance in random populations.

The problems of homogeneity and complexity of aggregation patterns in natural populations are discussed. It is pointed out that many natural populations are non-homogeneous and may be characterized by complex aggregation patterns. When these conditions prevail, the aggregation indices will yield a measure of over-all aggregation that represents an average of all the conditions present in the populations.

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PHENOLOGICAL OBSERVATIONS OF NINETEEN NATIVE TREE SPECIES IN NORTHEASTERN MINNESOTA

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It is becoming increasingly important that agencies working with forests fully understand the seasonal behavior of trees with which they work. Vegetative and reproductive responses of different tree species vary considerably from year to year. An understanding of how these variations occur is important to the tree breeder who must know each year when to expect the periods of flower, seed harvest, and—for grafting work—the period of cambial activity. It is important to the entomologist who is interested in the developmental stages of tree growth which correlate with insect cycles. It is of interest to the plant physiologist who is concerned with the factors which control tree growth and differentiation. It is of concern to ecologists as a factor in plant succession and in other ways.

Records of phenological responses in other areas have appeared in the literature (Gill 1955, Hodson 1951, Lindsey and Newman 1956). However, since phenological responses vary greatly from one region to the next, it was felt that a review of this literature would not pertain directly to the data presented in this paper. A general review of phenological findings for given species throughout the country would be of importance, but is not

within the scope of this paper. This paper presents the results of a 5 year study of major seasonal changes in the native tree species in northeastern Minnesota. The study was carried out within the 160 acre area of the Quetico-Superior Wilderness Research Center, a privately sponsored laboratory on Basswood Lake in the roadless portion of the Superior National Forest.

Five trees of flower-producing age were selected for each of the 19 native species studied. Wherever possible, trees of different size classes were used. Effort was made to select trees growing on sites which differed with respect to drainage, exposure, and degree of stand density. Hence, some trees were situated on well-drained, sandy loam soil and were exposed to good conditions of light and aeration. Others were located on shaded, moist clay sites with less aeration. The tamaracks were in a peat swamp. Average specimens of each species were chosen; any trees showing abnormally rapid or slow growth, disease, insect, or other damage were eliminated. Records have been kept for 5 years since the winter of 1951 and are being continued.

A dendrometer station was set up at breast height on the north side of each tree. Micrometer

dial indicator no. 262 dendrometer was used in daily, morning readings at these stations during the growing season. In spring, readings were begun in the period just before the first crown activity was observed in any of the trees and were continued until the last stage of vegetative or reproductive activity was completed. Thereafter until cambial activity ceased, readings were taken every 3 days. Daily records of vegetative and reproductive activity were also kept. The analysis presented in this paper, however, uses only the range of dates on which the initial activity in each developmental stage occurred. Thus, initial bud swell refers to the first noticeable bud enlargement in any part of the tree crown. Initial leaf refers to the emergence of the first leaves in recognizable form. In application to the conifers, this refers to the stage in which the needles are first observed protruding from the sheath. Initial flowers refers to the stage in which a recognizable flower is first observed in any part of the crown. Initial pollen refers to the stage in which pollen dispersal is first noted from any part of the crown.

Temperature was recorded with a Taylor recording thermograph. For the purposes of this analysis, the maximum and minimum daily temperatures were used. Rainfall was determined with a standard rain gauge. During the 5 years of this study, the spring season varied from extremely early and warm to very late and cold.

RESULTS

A summary of some of the major observations is presented in Table 1. As stated in the table heading, it should be emphasized that the 2 dates in each square are the earliest and latest dates on which that activity was noted in any of the 5 years of the study. Figure 1 gives the temperature record for the 5 year period, together with the annual dates of initial bud and cambial activity. From these, the following consistencies can be noted:

Fraxinus nigra Marsh., black ash: Initial vegetative bud activity and flowering began after a period of at least 5 days of minimum temperatures above freezing and during a spring rise of maximum temperatures to above 70 degrees. In most cases, stem expansion was closely associated with initial bud swell.

Fraxinus pennsylvanica Marsh., red ash: Red ash followed a time pattern similar or 1-4 days earlier than that of black ash. However, abrupt increase in stem expansion was associated with extreme rise in temperature. This was not noted in black ash.

Ulmus americana L., American elm: Flowering began during or up to 10 days before vegetative

bud activity. The latter usually preceded the major period of stem expansion.

Pyrus americana (Marsh.) DC., mountain ash: Bud expansion usually was observed first during or soon after the first spring period in which maximum temperatures were between 60 and 65° F, and minimum temperatures were still below freezing. This was well in advance of the onset of stem expansion. Early in the period of stem expansion, leaf development began and was followed, after a period of 2-6 days, by flowering. The sequence of bud swell, leafing, flowering, and stem expansion was relatively consistent from year to year; except for initial activities, it did not appear to be influenced by early spring temperature extremes.

Quercus macrocarpa Michx., bur oak: Flowering followed leaf expansion, before or early in the major increase in stem expansion.

Tilia americana L., basswood: Initial bud swell was 1 or more weeks earlier than that in oak, although leafing began at the same time in both. Usually, vegetative bud swell began before stem expansion, but reproductive activities took place during the period of greatest stem expansion. Flowering occurred 1-4 weeks after leafing.

Populus tremuloides Michx., quaking aspen: Flowering and vegetative bud swell were simultaneous, beginning prior to the major increase in stem expansion. Stem expansion frequently fluctuated with early spring temperature fluctuations.

Populus grandidentata Michx., large-toothed aspen: The responses corresponded in sequence with those of quaking aspen but were frequently 1-3 weeks later.

Betula papyrifera Marsh., paper birch: Vegetative bud activity and staminate flower development were often initiated in very cool weather when temperatures were below 65°F. maximum with minimums below freezing. About 3 weeks later, still before the onset of stem expansion, pollination took place. A correlation exists between abrupt increase and decrease in stem expansion and sudden rise and fall of temperature in spring and autumn.

Betula lutea Michx., yellow birch: Responses were in the same sequence as those of paper birch, but development was slower. Variations in stem expansion were associated with sudden rise and fall of temperature.

Acer saccharinum L., silver maple: Bud activity began during the first gradual increase but before the rapid climb in stem expansion. Flowering preceded vegetative bud activity by about 1 week.

Acer rubrum L., red maple: Vegetative and reproductive responses were simultaneous with

TABLE I: A summary of the major phenological activities of 19 native tree species in northeastern Minnesota. The number representing the month precedes that for the day. In each square, the upper date is the earliest date on which the response was observed on any tree of that species during the 5 year period (1951-1956); the lower date is the latest date on which the response was first observed. Where one date is given, only one year's observations were obtained

Species	INITIAL ACTIVITY				Seed fall	Leaf color change	Leaf fall	CAMBIAL ACTIVITY	
	Bud	Leaf	Flower	Pollen				Initial	End
White Spruce.....	4/ 4 5/15	5/17 6/ 9	4/29 5/28	5/12 6/ 1	9/ 5 9/17			4/21 5/ 7	9/ 2 9/13
Black Spruce.....	4/12 5/15	6/ 2 6/19	5/ 6 5/20	5/15 6/ 6				5/13 5/21	7/28 8/11
Balsam Fir.....	4/ 4 5/20	5/17 6/ 3	4/30 5/ 8	5/25 6/ 4	 10/ 3			4/ 6 5/20	7/28 9/10
White Pine.....	4/ 6 5/11	5/19 6/23	5/20 5/28	6/ 7 6/26	 10/ 3			5/ 3 5/20	8/ 9 9/7
Red Pine.....	4/ 2 4/15	5/10 6/24	5/ 9 5/24	5/26 6/14	 8/29			5/ 3 5/20	7/30 9/ 7
Tamarack.....	4/ 6 4/23	4/21 5/16	4/25 5/ 9			10/ 6 10/10	10/ 8 10/18	4/ 6 6/ 8	7/29 8/ 6
Cedar.....	 5/ 1	 6/18	4/10 5/ 6	4/27 6/ 4	9/26 10/ 4			5/ 7 5/23	7/ 5 8/29
Black Ash.....	4/27 5/25	5/20 6/ 8	4/27 5/25	5/19 6/ 5	 10/ 3	8/29 9/13	9/19 10/ 3	5/ 5 5/21	6/20 8/11
Red Ash.....	4/24 5/25	5/10 6/ 3	4/23 5/25	5/12 6/ 4	 10/ 3	9/ 6 9/20	9/19 10/ 3	5/ 6 5/20	7/ 7 7/30
Mountain Ash.....	4/24 5/ 1	4/30 5/21	5/ 2 6/ 1	6/13 6/16	8/20 9/17	8/20 9/ 3	8/29 10/ 8	5/15 6/ 5	7/22 8/ 5
American Elm.....	4/21 5/16	5/ 6 5/29	4/25 5/ 8	5/ 4 5/11		9/16 10/ 4	10/ 3 10/22	5/14 6/25	7/ 8 8/13
Bur Oak.....	4/24 5/21	5/11 5/25	5/12 6/ 2	5/23 6/ 8	 10/ 3	9/13 9/19	9/26 10/14	5/15 5/29	7/16 8/23
Basswood.....	4/21 5/ 5	5/11 5/25	5/24 6/28	6/22 6/28	10/ 3 10/14	9/16 9/20	9/20 10/10	5/16 5/25	7/17 7/28
Quaking Aspen...	4/ 2 4/30	4/27 5/21	4/14 4/24	4/29 5/ 5	5/ 9 6/12	9/26 10/ 4	10/ 4 10/14	4/28 5/23	8/ 4 9/ 3
Bigtoothed Aspen.	4/24 5/11	5/19 6/ 8	4/23 5/15	5/ 5 5/18	6/10 6/17	9/20 10/ 4	10/ 4 10/14	5/14 5/22	8/ 4 9/ 3
Paper Birch.....	4/ 6 5/ 5	4/29 5/21	4/ 2 4/23	4/28 5/21	 8/10	9/16 9/26	9/26 10/10	5/ 3 5/21	8/ 4 8/29
Yellow Birch.....	4/ 6 5/ 1	5/ 3 5/25	4/ 2 5/16	5/13 5/29	 8/ 6	8/29 9/26	9/26 10/ 4	5/ 4 5/20	7/30 8/12
Silver Maple.....	4/21 5/13	4/30 5/25	4/18 4/30	 4/21	 5/17	 9/26	10/ 3 10/ 4	4/22 5/20	7/ 1 8/11
Red Maple.....	4/21 5/11	4/27 5/18	4/18 4/30	 5/ 7		9/16 10/ 4	10/ 4 10/14	5/ 2 6/ 3	7/ 6 7/30

those of silver maple. Stem expansion, however, often began 1 week or more later.

Picea glauca (Moench) Voss, white spruce: Vegetative bud swell and flowering frequently overlapped, usually following a rise in maximum temperatures to 70°F. or above after minimums

had remained above freezing for more than 1 week. Pollen shed was followed by initial leafing, early in the gradual or abrupt rise in stem expansion. Increase and decrease in stem expansion correlated with sudden rise and fall in temperature in the springtime.

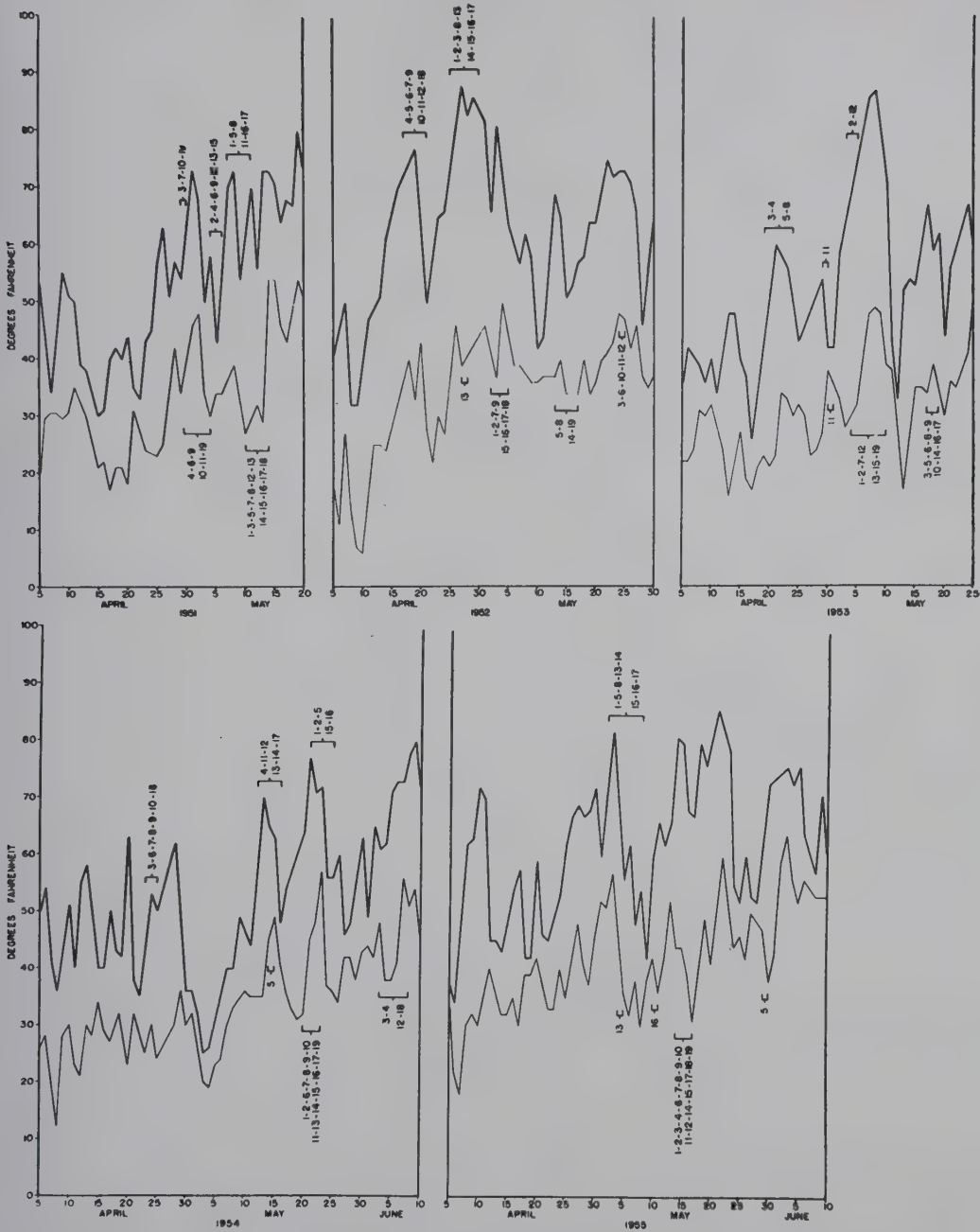


FIG. 1. The relation between maximum and minimum temperatures and initial spring bud and cambial responses. The upper heavy line represents maximum temperatures; the lower, lighter line represents minimum temperatures. The numbers above the temperature lines indicate tree species for which the initial bud activity occurs on that date. The numbers below the lines refer to species for which initial cambial activity occurs on that date. The numbers refer to the following species: 1.—black ash 2.—red ash 3.—mountain ash 4.—American elm 5.—bur oak 6.—basswood 7.—quaking aspen 8.—large-toothed aspen 9.—paper birch 10.—yellow birch 11.—silver maple 12.—red maple 13.—white spruce 14.—black spruce 15.—balsam fir 16.—white pine 17.—red pine 18.—tamarack 19.—northern white cedar.

Picea mariana (Mill.) BSP., black spruce: In general, development was at the same time or within a week after that of white spruce. As with white spruce, abrupt changes in stem expansion were associated with sudden fluctuations in temperature.

Abies balsamea (L.) Mill., balsam fir: Bud swell and flowering occurred together, after temperatures had risen to above 70°F. maximum with minimum temperatures above freezing for 1 week or more. Pollen shed and leafing were also simultaneous. The vegetative and reproductive responses were closely associated with the abrupt spring increase in stem expansion. Abrupt changes in stem expansion were frequent in periods of sudden change in temperature.

Pinus strobus L., white pine: Vegetative and reproductive responses were observed in the abrupt spring increase in stem expansion. Bud swell usually followed maximum temperatures of 75°F., after minimum temperatures had been well above freezing for 1 week or more.

Pinus resinosa Ait., red pine: Vegetative responses were almost always about 1 week earlier than those of white pine. Flowering and pollen shed preceded leafing and began 1-2 weeks before that of white pine. These responses occurred early in the period of abrupt stem expansion. During May and June, variations in stem expansion were associated with sudden, large temperature changes.

Larix laricina (Du Roi) K. Koch, tamarack: Bud swell began relatively early and, unlike that in many other species, was not consistently correlated with spring warm spells. Leaf and flower development overlapped. Throughout the period of rapid growth, irregularities in stem expansion were associated with extreme fluctuations in temperature.

Thuja occidentalis L., northern white cedar: Reproductive responses preceded vegetative responses, both preceding the initial spring increase in stem expansion. In late spring and fall, irregularities in stem expansion frequently correlated with temperature changes.

DISCUSSION

Dates of initial phenological responses (Table I) may vary as much as a month from year to year. This wide variation seems to indicate that factors other than those relatively stable from year to year, such as photoperiod and light intensity, must be influential in the seasonal development of these species. Because of this, an attempt was made to discover any correlations between developmental stages and certain weather conditions. It would be logical to assume that changes in tem-

perature and moisture would have an effect on the timing and amount of growth. In the results obtained, frequent correlations are found between certain types of growth activities and certain weather conditions. It is not within the scope of this paper to infer or determine whether these correlations indicate control or causality. However, the most striking correlations might bear further investigation and are discussed below.

Temperature and initial bud swell

As shown in Figure 1, many of the species begin bud activity during or shortly after a warm period. Certain species show consistencies as to the temperature ranges in which this bud swell begins. Mountain ash, quaking aspen, yellow birch, and paper birch begin activity in the first spring warm spell when minimum temperatures may still be below freezing or have not been above freezing for more than 3 days. However, white and black spruce and red pine begin activity during the first warm spell after minimum temperatures have reached 30°F. or above. American elm and red maple never begin activity until after maximum temperatures have reached 60°F. or above, while black ash, red ash, balsam fir, and white pine begin activity after maximum temperatures have reached 70°F. or more.

Bud swell in basswood, bur oak, large-toothed aspen, and silver maple occurred over a wide range of temperatures. It was observed, however, that bud swell in large-toothed aspen nearly always was 1 week later than that in quaking aspen. If, therefore, certain levels of temperature are required for initiation of spring bud activity, it may be that some species respond more slowly than others to the initial stimulus and that, therefore, these trees are responding to an earlier temperature level. It is also possible that for other species the temperature levels which occur immediately before and during the period of activity are not the critical ones in stimulating that response, but rather that the important temperatures occur earlier.

In none of the species studied was there any consistent correlation between initiation of either flowering or leafing and certain current temperature levels. It would appear that these processes require no further temperature stimulus and follow bud swell within a period of time which varies with the species, but within which time there can be a range of temperatures. Since responses of any one species varied several weeks from one year to the next, it would appear that an exact photoperiod is not a critical factor in determining the time of any of these responses.

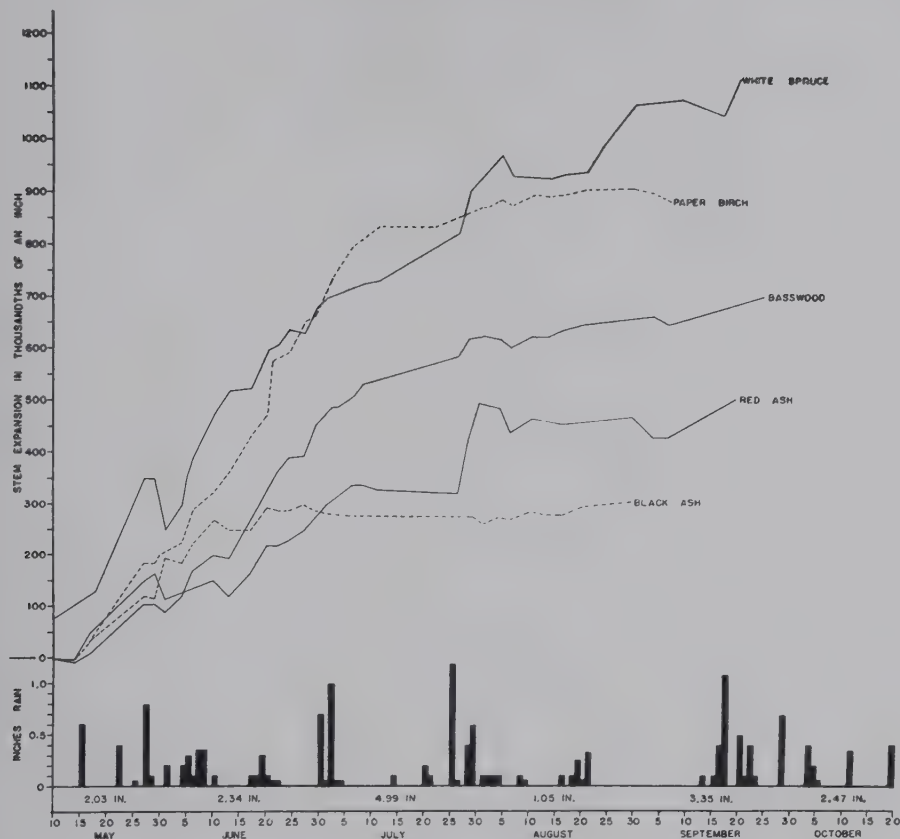


FIG. 2. Stem expansion in relation to rainfall. The broken lines represent species which show little or no correlation of stem expansion with rainfall. The numbers immediately below the rainfall bars indicate the total monthly precipitation.

Temperature, rainfall, and stem expansion

The dendrometer readings record changes in the diameter of the stem. It must be recognized that a woody stem may decrease or increase in diameter because of temporary swelling caused by excessive moisture or heat. However, the basic curve of stem expansion (Fig. 2) gives a typical growth curve and indicates both the periods of relatively active growth and relative dormancy.

Stem expansion in all species studied fell into 3 periods: 1. Early spring period of dormancy or very gradual increase. 2. Period of rapid increase in stem diameter. 3. The mid-summer period of decreasing expansion rate. A few illustrations of this sequence can be seen in Figure 2. The dates on which the major increase in cambial activity began are noted in Figure 1. Although many of these increases began after a rise in temperature, there was no definite, consistent temperature level characteristic for increase in any particular spe-

cies. In general, however, the period of onset of cambial activity began after maximum temperatures were 70°F. or more and minimum temperatures were above freezing.

In several species, stem diameter changed abruptly in close association with sharp changes in temperature throughout the growing season. This relationship was particularly evident in red ash, quaking aspen, paper birch, yellow birch, white spruce, black spruce, balsam fir, red pine, tamarack, and northern white cedar.

In many species, a very close correlation was found between heavy rainfall (1 inch or more) and abrupt increase in stem expansion throughout the growing season (see Figure 2). The apparent influence of rain was most obvious in red ash, American elm, mountain ash, basswood, yellow birch, white spruce, black spruce, balsam fir, and northern white cedar. No attempt was made to determine whether this increase was caused by

actual growth or by temporary water swelling. However, as can be seen in Figure 2, in some cases a decrease in stem diameter was noted several days after the rain, indicating a temporary swelling.

Sequence of spring responses

The sequence of spring vegetative and reproductive responses varied among the species studied. In general, four types were noted:

1. Flowering always preceded vegetative bud swell in silver maple, red maple, and northern white cedar.

2. Flowering always followed vegetative bud swell but preceded initial leafing in black ash, white spruce, black spruce, balsam fir, white pine, and red pine.

3. Flowering followed initial leaf in bur oak, basswood, mountain ash, and tamarack.

4. Vegetative bud swell and flowering occurred simultaneously in quaking aspen, large-toothed aspen, paper birch, yellow birch, red ash, and American elm.

The relation between flowering and bud swell and the onset of rapid stem expansion also varied among species. In American elm, mountain ash, white birch, yellow birch, silver maple, and red maple these responses occurred before the initial increase in stem expansion. However, in black ash, red ash, white spruce, black spruce, balsam fir, white pine, red pine, and tamarack, they occurred during the period of rapid stem expansion.

SUMMARY

The phenological responses of 19 native tree species in northeastern Minnesota were recorded for 5 years. Species studied include: black ash, red ash, mountain ash, American elm, bur oak, basswood, quaking aspen, large-toothed aspen, paper birch, yellow birch, silver maple, red maple, white spruce, black spruce, balsam fir, white pine,

red pine, tamarack, and northern white cedar. Responses observed were: bud swell, leafing, flowering, pollination, seed fall, leaf color change, leaf fall, stem expansion. It was found that mountain ash, quaking aspen, yellow birch, and paper birch began spring activity in the first warm period when minimum temperatures may still be below freezing. White spruce, black spruce, and red pine begin activity after minimum temperatures have reached 30°F. or above. American elm and red maple begin activity after maximum temperatures have reached 60°F. or above, while black ash, red ash, balsam fir, and white pine begin activity after maximum temperatures have reached 70°F. or more. Initial spring activity in basswood, bur oak, large-toothed aspen, and sugar maple, seems unrelated to any specific temperatures. In the species studied, no obvious correlation appears between current temperature levels and the beginning of either flowering or leafing.

Stem expansion frequently fluctuated with abrupt changes in temperature and rainfall. Aside from these temporary fluctuations, however, a typical growth curve was obtained for all species. In most species, the period of onset of cambial activity began after maximum temperatures were 70°F. or more and minimums were above freezing. Dates of some phenological responses may vary as much as one month from one year to the next.

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SOIL MICROFUNGI IN RELATION TO THE PRAIRIE CONTINUUM IN WISCONSIN¹

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This study is one of a series of investigations into the ecological relationships of the soil micro-

flora with the associations of higher plants occurring in Wisconsin. An earlier study, Tresner, et al. (1954), dealt with the soil microfungal populations in the upland forests of the prairie-forest border region of southern Wisconsin.

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twenty-five prairie stands distributed through 12 counties in the central and southern portions of Wisconsin. The stands were chosen from among those which have been characterized sociologically on the basis of their higher vegetational composition by Curtis and Greene (1950) and by Curtis (1955). None of the stands was less than four acres in extent and all were selected from areas known to have been prairie at the time of European settlement (ca. 115 years ago), as shown by the original land survey. The prairie stands represent relics of the original vegetation and are located along railroad rights-of-way, on flats with thin soil, steep hillsides, low grounds and other sites not suitable for agriculture or pasturage. So far as is known they have not been disturbed violently either by plowing or grazing, although undoubtedly most have been burned or cut for hay occasionally.

In their study of 65 Wisconsin prairie stands it was concluded by Curtis and Greene (1950) that there are no discrete plant communities in the stands of vegetation studied. Further work was undertaken by Curtis (1955) to determine whether or not prairie vegetation consisted of a continuum of continuously varying ranges of species tolerance such as had been demonstrated for the upland forest of southern Wisconsin (Curtis and McIntosh 1951). Presence lists of all species of higher plants for 157 prairie stands were obtained. Certain plants showed a preference for a particular topographic type of prairie but none was restricted to a single type. A species exhibiting a preference for one type of prairie at least 10% greater than for any other was termed an indicator species. A group of indicator species was established for each type of prairie according to landform, whether wet, wet-mesic, mesic, mesic-dry, or dry.

Each prairie stand was given an index number. This was done by summing the weighted numbers of indicator species of each type in the stand and dividing by the total number of indicator species in the stand. The range of index numbers obtained fell between 100 and 500. The wet prairies were represented by the lower index numbers, the dry prairies by the higher numbers, and the mesic prairies by the intermediate values. When the stands were arranged in order according to their index numbers it was found that the individual plant species formed smooth curves of occurrence with peaks of presence in a restricted portion of the index range. Some species were found to have broad amplitudes of occurrence while others were rather limited. However, the species constituents formed a continuous series from those

of the wet sites to those of the dry sites. It was concluded, therefore, that the prairie stands form a vegetational continuum with no discrete vegetational communities.

In order to obtain an over-all view of the characteristic soil microfungal populations in these Wisconsin prairies, the twenty-five stands analyzed in the present study were selected from the series with some of each type of prairie represented. Their continuum index (C.I.) numbers ranged from 100 to 445.7. Most of the prairies were sampled only once, although one stand was sampled three times while a second was sampled four times in connection with other experiments.

MATERIALS AND METHODS

The soil sampling methods, isolation methods, and analytical determinations employed in the present investigation were, for the most part, closely patterned after those utilized by Tresner et al. (1954).

From each of the twenty-five prairies dealt with, six vial samples of soil were collected for microbiological analysis; at the same time a duplicate set of samples in soil cans was secured for use in determining soil moisture. All samples were taken from the A₁ horizon at approximately one inch below the surface, and each set of six was obtained along a transect through a given prairie. The vial samples were processed either immediately following delivery at the laboratory or after sub-zero storage for various periods of time.

Estimates on the numbers of bacteria and actinomycetes per gram of dry soil were arrived at by the method of Tresner et al. (1954). In dealing with the fungal populations the methods of the same authors were also closely followed, save that the isolation medium employed was unacidified soil extract agar to which had been added rose bengal dye at the rate of 1/30,000 and streptomycin to give a concentration of 30 gamma of the antibiotic per ml. Seeding of the plates was carried out using soil suspensions at a dilution of 1/10,000 except in the case of samples from seven wet prairies, where a lower dilution was required. After colony counts had been obtained, pure cultures were set up on potato-dextrose agar tube slants to provide a basis for identification and for computing species frequencies. Thirty random isolates were taken from each soil sample for this purpose (180 isolates, in all, from each prairie stand).

Valuable help in the identification work was given by authorities on particular fungal groups. Professor W. C. Snyder of the University of California kindly identified a number of repre-

sentative *Fusarium* isolates which the writers submitted to him and he verified their determinations on others. Dr. G. R. Bisby of the Commonwealth Mycological Institute, Kew, Surrey, England, checked several isolates of *Stachybotrys*, while Mr. N. C. Preston of the Ministry of Agriculture and Fisheries, Wolverhampton, Staffordshire, England, aided in the identification of *Myrothecium* cultures. Professors M. P. Backus and K. B. Raper of the University of Wisconsin, Dr. C. W. Hesseltine of the USDA Northern Utilization Research Branch at Peoria, Illinois, Professor R. B. Korf of Cornell University, Dr. C. W. Emmons of the National Institute of Health, Bethesda, Maryland, and Dr. R. G. Atkinson of the Laboratory of Plant Pathology, St. Catharines, Ontario, also rendered assistance of one sort or another, and their aid is gratefully acknowledged.

Among the fungi isolated in this study were six species new to science, several species not previously recorded as soil inhabitants or unreported from Wisconsin, and a few of special interest for other reasons. One of the new species, *Penicillium megasporum*, has already been described in the literature (Orpurt and Fennell 1955). The remaining forms will be considered in detail in another publication. Stock cultures of all of these entities are being maintained.

RESULTS

Species distribution

The ecological analysis of the microfungal flora of prairie soils consisted of ascertaining frequency distribution patterns for nearly one hundred species of soil fungi. As an analytical factor, frequency determines the commonness of occurrence of a species, which when related to the prairie continuum afforded a ready means for assessing the interrelationships of organisms and environment. Following the precedent set in the upland-forest microfungal studies, arbitrary limits were set on which species were to be considered. Those species which occurred at a frequency of 50% or higher in one or more stands during the study or which were encountered in four or more sampling sites (insofar as it was feasible to determine) but at lesser frequencies, were included in the present ecological study.

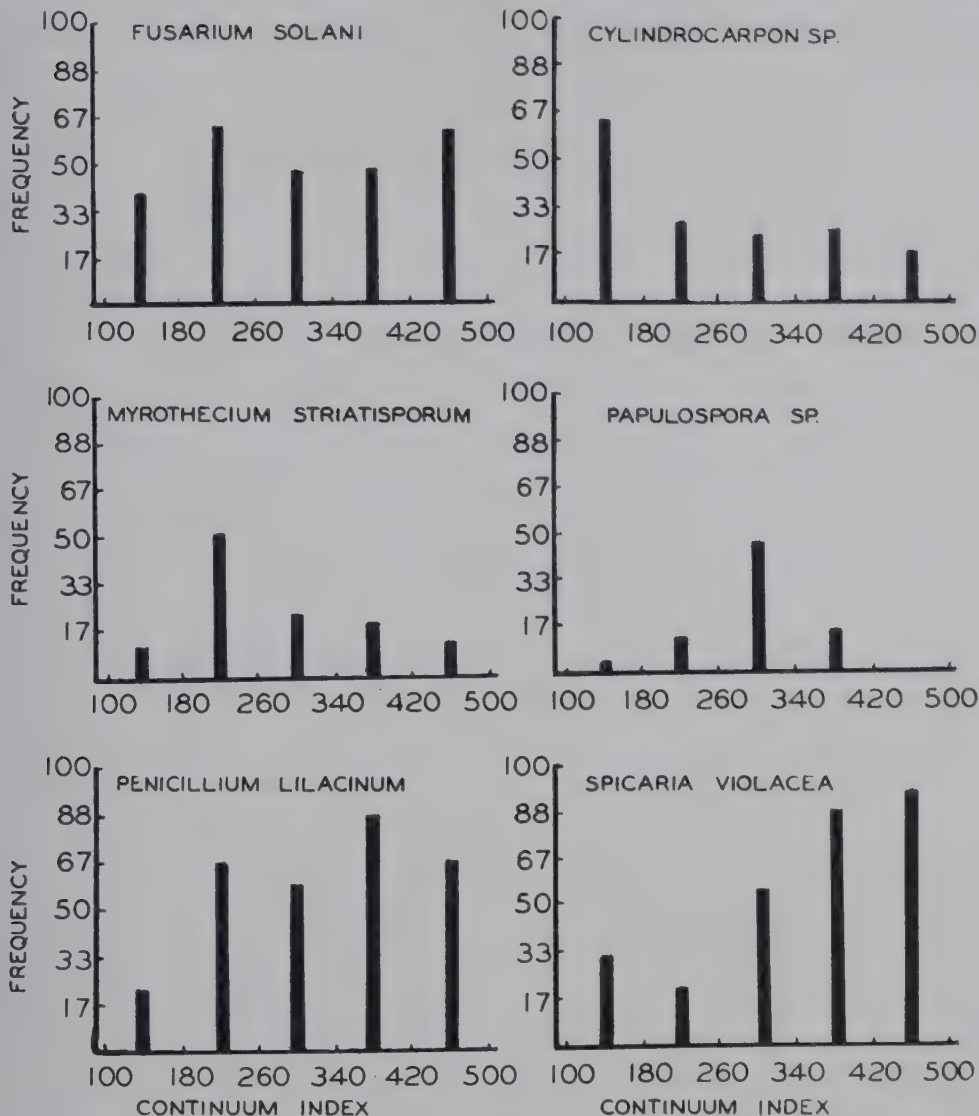
A pattern of distribution for each species was obtained in the following manner. The stands were assigned a continuum index number on the basis of their higher plant constituents (Curtis 1955), and were arranged in the numerical order of this index. The full range was divided into five equal intervals of 80 units each (100-180, 180-260, etc.). The frequencies at which a particular fun-

gus species occurred in each stand were recorded along the continuum. Frequencies within each group of stands in each interval were averaged. For example, *Fusarium solani* occurred at frequencies of 17, 33, 50, 50, 17, 0, and 100 in stands in the continuum interval 100-180. These percentages were summed and divided by 7 (the number of stands) to give an average frequency of 38.1% for the interval. Average frequencies for *F. solani* were calculated in a similar way for each of the remaining four intervals. When these averages were plotted the pattern shown in Figure 1 resulted. Figures 2, 3, 4, 5, and 6 show curves obtained by plotting the average frequencies of other representative species.

A large portion of the species concerned had very broad amplitudes of occurrence along the prairie continuum. A few of these (e.g. *Fusarium solani*, Fig. 1) were ubiquitous in that they appeared to be about as prevalent in one prairie type as in another. In contrast, other species of broad amplitude exhibited a well-defined frequency crest and these have been characterized according to the interval in which this peak occurred. Thus, *Cy-*

TABLE I. Microfungal species of limited amplitude

SPECIES		AVERAGE FREQUENCY PER CONTINUUM INTERVAL					CI Range
Culture No.	Name	100-180	180-280	280-340	340-420	420-500	
WET PRAIRIES							
47	<i>Emericellopsis</i> n. sp.	33	..	..	..	..	100-161
90	<i>Phoma</i> sp.	33	..	..	..	..	100-176
57	<i>Mycelia sterilia</i>	26	..	..	..	..	133-176
75	<i>Alternaria tenuissima</i>	26	..	..	..	..	100-161
15	<i>Cephalosporium</i> sp.	14	..	..	..	..	100-176
16	<i>Spicaria</i> sp.	12	..	..	..	..	100-161
42	<i>Sporotrichum</i> sp.	12	..	..	..	..	100-161
93	<i>Mycelia sterilia</i>	7	6	..	..	..	133-242
39	<i>Mycelia sterilia</i>	7	6	..	..	..	100-242
92	<i>Cephalosporium</i> sp.	28	27	3	..	..	100-271
WET-MESIC PRAIRIES							
73	<i>Thielaviopsis</i> sp.	7	33	17	..	..	176-311
14	<i>Penicillium stoloniferum</i> ..	..	33	..	..	..	249
MESIC PRAIRIES							
30	<i>Mucor hiemalis</i>	2	11	14	..	..	129-311
33	<i>Cunninghamella elegans</i> ..	2	6	11	..	..	161-343
17	<i>Pseudogymnosascus roseus</i> ..	..	11	33	..	..	242-317
1	<i>Penicillium thomii</i>	..	6	11	..	..	242-338
31	<i>Absidia glauca</i>	..	6	8	..	..	217-338
7	<i>Penicillium purpurogenum</i> ..	..	..	11	..	..	309-338
56	<i>Stachybotrys</i> n. sp.	..	..	8	..	..	309-318
9	<i>Penicillium raistrickii</i>	..	..	6	6	..	297-387
76	<i>Alternaria tenuis</i>	..	..	28	22	22	297-425
DRY-MESIC PRAIRIES							
24	<i>Aspergillus terreus</i>	..	..	3	25	11	297-392
11	<i>Penicillium roseo-purpureum</i>	..	..	11	22	..	309-387
63	<i>Myrothecium striatisporum</i> ..	..	..	..	18	..	309-311
DRY PRAIRIES							
84	<i>Cephalosporium</i> sp.	..	..	..	3	33	425-446
94	<i>Mycelia sterilia</i>	..	..	..	..	50	443-446
91	<i>Phialophora</i> sp.	..	..	..	..	16	443



FIGS. 1-6. Average frequency of selected species arranged according to continuum index intervals. 1 (upper left). A "ubiquitous" species. 2 (upper right). A "wet prairie species." 3 (middle left). A "wet-mesic prairie species." 4 (middle right). A "mesic prairie species." 5 (lower left). A "mesic-dry prairie species." 6 (lower right). A "dry prairie species."

lindrocarpon sp. (Fig. 2) which showed a high frequency in the first continuum interval (C.I. 100-180) has been designated as a "wet prairie species"—even though it was also found with lower frequencies in all of the other intervals. In similar manner, *Myrothecium striatisporum* (Fig. 3) is referred to as a "wet-mesic prairie species," *Papulospora* sp. (Fig. 4) as a "mesic prairie species," and *Spicaria violacea* (Fig. 6) as a "dry

prairie species." The distributional patterns exhibited in these cases suggest that the species in question have broad tolerance but nevertheless display a preference for the soil environment of a particular type of prairie.

Roughly one fourth of the species dealt with showed restricted amplitudes (Table I)—several, indeed, having been encountered in only one of the five intervals.

As indicated previously, the average frequencies for all species represented were determined. Excluding the ubiquitous forms, all the remaining species were sorted into five groups according to the interval in which each reached its frequency crest, and the members of each group were further arranged according to the relative height of the crest. Table II shows the listing of twenty-three selected examples. The broad amplitudes which most of these possess made them especially valuable as a framework on which the remaining species could be fitted. Table III contains the frequencies of all species of the study with the species arranged by intervals according to the occurrence of their maximum average frequencies. The ubiquitous species are included in this table in the mesic (C.I. 260-340) interval. Culture numbers as well as species names are used in this table, since in many cases an exact species determination has not been possible. The intervals have been named wet prairie, wet-mesic prairie, etc., but it should not be assumed that these refer to discrete biological units. They are merely arbitrary segments of a continuous ordination.

Numbers of species and special groups

During the course of the study it was noticed

TABLE II. An arrangement of twenty-three species according to the interval in which each reached its highest frequency

Species	AVERAGE FREQUENCY (Percent)				
	Continuum Intervals				
	100-180	180-260	260-340	340-420	420-500
WET PRAIRIES					
<i>Trichoderma viride</i>	60	50	45	42	6
<i>Cylindrocarpon</i> sp.....	66	28	22	25	17
<i>Cladosporium herbarum</i>	48	39	42	28	33
<i>Verticillium</i> sp.....	58	16	20		
WET-MESIC PRAIRIES					
<i>Mortierella</i> sp.....	36	56	47	45	45
<i>Myrothecium striatisporum</i>	10	50	22	20	11
<i>Penicillium javanicum</i>	5	55	11	16	22
<i>Cephalosporium</i> sp.....	2	28	14	11	
MESIC PRAIRIES					
<i>Fusarium oxysporum</i>	19	16	64	50	50
<i>Papulospora</i> n. sp.....	2	11	46	16	
<i>Acrostalagus</i> sp.....	24	28	42	14	16
<i>Penicillium nigricans</i>	10	11	42	6	28
<i>Penicillium variable</i>	22	22	42	22	11
<i>Penicillium janthinellum</i>	17	17	59	8	
<i>Penicillium restrictum</i>	5	22	58	11	22
<i>Botrytis</i> sp.....	10	28	51	31	11
DRY-MESIC PRAIRIES					
<i>Penicillium lilacinum</i>	21	67	58	88	67
<i>Aspergillus terreus</i>			3	85	11
<i>Penicillium funiculosum</i>	14	28	36	47	22
DRY PRAIRIES					
<i>Spicaria violacea</i>	31	22	56	83	89
<i>Aspergillus fumigatus</i>	17	59	34	61	78
<i>Trichidium</i> sp.....	7	56	35	44	72
<i>Mucetia sterilia</i>	19	33	45	42	61

that there were some variations in the number of species of fungi occurring in the various prairie stands. However, since the stands were sampled at random, it was not possible to detect any particular trend until all the data had been brought together and summarized.

To ascertain whether there were any differences in the number of species along the gradient of the prairie continuum, the average number of species encountered in each of the five intervals previously defined was determined (Table IV). The values indicate that the highest number of species occurs in the mesic interval and that the number of species falls off in either direction. This may be explained by the overlapping of "wet" species and of "dry" species into the mesic interval, therefore increasing the value for that interval. Essentially the same distribution has been found for the species of higher plants occurring on the prairies, and for the herbaceous species and microfungal flora of the upland-hardwood forest in southern Wisconsin.

The distributional patterns of larger taxonomic groups of fungi were found to reflect the influence of the soil environment along the prairie continuum. The number of species of *Penicillia*, *Mucorales*, *Fusaria* and *Aspergilli* for each stand may be found in Table IV together with the average percent of total species per interval for each particular group. The *Penicillia* as a whole were characterized as typically mesic, although the genus was also represented in a substantial manner in both the wet and dry prairies. The *Mucorales* exhibited a rather ill-defined preference for the wet-mesic interval but were present in all types of prairies. The *Fusaria* were obviously non-preferential as to type of prairie soil environment. The figures for the *Fusaria* were based primarily on data from two species, *F. solani* and *F. oxysporum*, both of which had wide amplitudes of soil environmental tolerances. The *Aspergilli* definitely increased towards the dry prairie end of the gradient.

Numbers of microorganisms

Certain trends in the numbers of fungi, actinomycetes and bacteria in the different prairies can be demonstrated. Quantitative data concerning microorganisms are subject to considerable variation from stand to stand and even from sampling site to sampling site on the same stand. Rose and Miller (1954) have established that fungal counts from soil samples taken from the same field frequently show variations of the order of 1:13 (50,000-641,000) per gram of soil. For actinomycetes the variation often exceeded 1:39

TABLE III. Frequency percent of microfungi in prairie soil

SPECIES																											Species Culture No.	
Culture	C. I.	100	128	133	143	150	161	176	217	242	249	271	297	309	311	318	338	343	357	387	392	393	405	425	442	446		
No.	Name Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		
WET PRAIRIES																												
36	<i>Trichoderma viride</i>	50	67	59	83	83	67	17	50	33	67	50	17	17	17	67	100	50	17	100	67	...	17	...	...	17	36	
46	<i>Cylindrocarpon</i> sp.....	67	50	83	83	33	33	100	50	33	...	17	17	...	33	33	33	17	17	50	33	33	...	33	17	...	46	
68	<i>Cladosporium herbarum</i>	83	83	17	67	...	17	33	33	33	50	67	17	17	17	33	33	83	67	...	17	50	33	...	83	...	17	68
87	<i>Fusarium</i> sp.....	67	...	67	17	50	...	67	...	...	...	...	...	...	33	33	...	...	...	...	...	...	17	...	...	...	87	
44	<i>Verticillium</i> sp.....	33	67	50	17	100	...	...	50	...	...	...	50	...	50	...	17	...	...	...	...	...	...	...	...	...	44	
54	<i>Cephalosporium</i> sp.....	50	67	17	...	33	50	50	...	...	...	50	...	17	...	...	...	...	...	...	33	33	...	...	...	...	54	
74	<i>Dematiaceae</i> sp.....	17	...	50	67	50	67	...	33	...	...	...	...	33	17	...	...	...	...	...	...	...	...	...	...	...	74	
47	<i>Emericellopsis</i> n. sp.....	100	...	33	67	...	33	...	...	...	...	...	...	...	...	...	...	...	...	...	17	50	33	...	83	...	47	
90	<i>Phoma</i> sp.....	100	33	...	50	...	17	33	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	90	
92	<i>Cephalosporium</i> sp.....	17	...	83	33	...	...	67	50	33	...	17	...	...	...	...	...	...	...	...	...	...	...	...	...	...	92	
22	<i>Volutella roseola</i>	17	67	50	17	17	17	...	...	...	...	...	...	...	33	17	...	...	...	...	...	...	...	...	...	...	22	
57	<i>Mycelia sterilia</i>	...	...	83	...	17	...	83	...	...	...	...	...	...	...	...	...	...	...	50	33	...	...	...	...	...	57	
75	<i>Alternaria tenuissima</i>	67	50	...	17	17	33	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	75	
60	<i>Myrothecia</i> sp.? <i>Coniothyrium</i> sp.....	100	17	17	...	50	...	17	17	...	...	33	...	...	17	...	17	...	...	...	17	...	...	33	...	...	60	
49	<i>Fusarium</i> sp.....	67	...	33	67	...	...	17	33	17	...	17	...	...	...	...	...	...	...	33	...	...	...	...	...	...	49	
64	<i>Myrothecium gramineum</i>	17	33	33	...	17	...	...	33	...	...	...	...	...	...	...	...	33	...	17	17	...	...	...	33	...	64	
88	<i>Spicaria</i> sp.....	17	17	...	33	...	33	...	33	...	...	17	...	...	17	...	...	33	...	...	...	...	...	33	...	...	88	
15	<i>Cephalosporium</i> sp.....	50	...	33	...	17	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	15	
16	<i>Spicaria</i> sp.....	17	17	...	50	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	16	
42	<i>Sporotrichum</i> sp.....	17	...	50	...	17	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	33	...	33	...	...	42	
93	<i>Mycelia sterilia</i>	...	...	50	...	...	...	...	17	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	93	
39	<i>Mycelia sterilia</i>	50	...	...	...	...	...	...	17	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	39	
41	<i>Chaetomium indicum</i>	17	...	17	...	...	...	...	17	...	...	...	...	17	...	...	...	...	...	...	...	...	...	...	...	...	41	
WET-MESIC PRAIRIES																												
96	<i>Mortierella</i> sp.....	17	33	17	50	33	17	83	67	67	33	67	33	33	67	50	33	17	17	17	100	100	17	17	67	50	96	
61	<i>Myrothecium striatissimum</i>	...	...	...	...	67	...	17	67	67	33	33	...	...	50	...	17	17	17	67	...	17	...	33	...	...	61	
5	<i>Penicillium javanicum</i>	...	...	...	...	33	33	...	33	67	50	...	...	...	...	...	17	17	...	67	...	17	...	33	...	33	5	
32	<i>Asidia spinosa</i>	100	17	...	17	...	50	...	17	33	...	17	17	17	17	...	17	17	...	33	...	...	...	...	...	...	32	
18	<i>Cephalosporium</i> sp.....	...	...	...	17	...	...	...	50	17	17	17	17	17	17	...	17	17	...	33	...	...	17	...	...	...	18	
95	<i>Stilbaceae</i> sp.....	...	...	...	...	...	...	...	67	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	95	
14	<i>Penicillium stoloniferum</i>	...	...	...	...	...	...	...	67	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	14	
73	<i>Thielaviopsis</i> sp.....	...	...	...	...	...	50	...	50	17	...	...	17	17	...	...	...	...	...	...	...	...	...	...	...	...	73	
MESIC PRAIRIES																												
50	<i>Fusarium oxysporum</i>	17	...	17	...	33	33	...	17	33	50	67	50	100	67	50	33	17	17	50	100	83	17	100	33	...	50	
78	<i>Papulospora</i> n. sp.....	...	...	...	17	...	17	...	17	17	17	17	50	67	33	83	17	67	17	...	...	...	...	...	...	...	78	
80	<i>Acrostagmus</i> sp.....	33	17	33	17	17	17	33	83	...	...	83	67	17	...	50	50	...	...	...	50	33	...	...	...	17	80	
10	<i>Penicillium nigricans</i>	...	...	...	...	67	...	...	...	33	17	83	50	33	33	83	...	17	...	...	17	...	67	17	...	...	10	
3	<i>Penicillium variable</i>	...	67	...	50	17	17	17	...	50	67	50	33	83	...	17	...	...	50	83	...	...	...	...	33	...	3	
6	<i>Penicillium janthinellum</i>	...	...	...	17	100	...	17	...	33	17	83	83	...	50	...	...	33	...	17	...	...	...	...	...	...	6	
4	<i>Penicillium restrictum</i>	...	...	...	17	17	...	33	33	67	33	50	33	...	17	...	50	...	...	...	...	17	67	...	...	...	4	
59	<i>Botrytis</i> sp.....	...	17	...	...	...	17	33	...	50	...	50	...	67	17	50	67	...	50	...	67	...	50	...	33	...	59	
28	<i>Asidia butleri</i>	33	...	...	...	33	...	17	17	...	...	17	33	...	50	...	67	...	17	...	...	...	...	17	...	...	28	
67	<i>Homodendrum</i> sp.....	17	...	...	...	...	...	33	...	...	...	50	50	...	...	67	...	...	...	...	...	...	...	...	...	...	67	
76	<i>Alternaria tenuis</i>	...	...	...	...	...	...	...	...	...	...	33	...	...	83	50	50	...	...	...	83	...	67	...	...	...	76	
2	<i>Penicillium simplicissimum</i>	17	...	50	...	...	...	...	...	...	50	67	...	33	...	...	...	...	...	...	...	...	...	...	...	...	2	
55	<i>Stachybotrys</i> n. sp.....	17	17	...	50	...	...	17	...	17	...	17	...	17	33	50	17	17	...	17	...	17	50	...	17	...	55	
72	<i>Zygorhynchus rulleimitti</i>	...	17	...	...	...	17	...	...	...	17	33	...	33	...	50	...	17	...	...	...	17	...	...	...	...	72	
72	<i>Sporormia leporina</i>	50	...	...	...	17	67	33	...	17	17	...	50	33	17	...	...	17	...	...	...	33	17	...	50	...	72	
65	<i>Mesobotrys</i> sp.....	...	...	17	...	...	...	...	...	17	50	...	17	...	33	33	33	17	...	...	17	...	...	...	...	...	65	
79	<i>Torula</i> sp.....	...	...	...	...	33	...	...	...	17	17	...	17	...	33	...	33	...	...	...	17	...	...	...	...	...	79	
17	<i>Pseudogymnoascus roseus</i>	...	...	...	...	...	...	...	33	...	17	...	17	...	67	17	...	...	...	...	...	...	...	...	...	...	17	
53	<i>Fusarium roseum</i>	17	...	...	...	...	...	...	...	...	17	...	17	...	...	...	...	...	17	...	...	...	...	...	...	...	53	
39	<i>Mucor hiemalis</i>	...	17	...	...	...	...	...	33	...	...	...	33	33	17	...	...	...	...	...	...	...	...	...	...	...	39	
7	<i>Penicillium purpurogenum</i>	...	...	...	...	...	...	...	...	...	...	...	17	...	17	...	50	...	...	...	...	...	...	...	...	...	7	
33	<i>Cunninghamella elegans</i>	...	...	...	...	17	...	17	...	...	...	...	17	33	17	...	...	33	...	...	...	...	...	...	...	...	33	
1	<i>Penicillium thomii</i>	...	...	...	...	...	...	17	...	...	...	...	17	...	33	...	33	...	...	...	...	...	...	...	...	...	1	
23	<i>Spicaria elegans</i>	...	17	17	17	...	...	17	...	17	33	...	17	...	...	17	...	...	...	...	17	...	...	...	...	...	23	
56	<i>Stachybotrys</i> n. sp.....	...	...	...	...	...	...	...	...	...	...	...	...	33	...	17	...	...	...	...	...	...	...	...	...	...	56	
77	<i>Papularia</i> sp.....	...	17	...	...	...	...	...	...	...	17	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	77	
31	<i>Asidia glauca</i>	...	...	...	...	...	...	17	...	...	...	...	...	17	33	...	17	33	...	...	...	...	...	...	...	...	31	
13	<i>Penicillium implicatum</i>	...	...	...	...	...	...	17	...	...	...	...	17	...	...	...	33	...	...	...	...	...	...	17	...	...	13	
9	<i>Penicillium raistrickii</i>	...	...	...	...	...	...	...	...	...	...	...	17	...	...	17	...	17	...	17	...	...	...	...	...	...	9	
DRY MESIC PRAIRIES																												
19	<i>Penicillium lilacinum</i>	...	67	...	83	...	83	67	50	50	50	50	...	100	50	100	100	67	50	100	100	83	67	67	67	...	19	

TABLE III (continued)

SPECIES																											Species Culture No.		
Culture No.	Name	C. I. Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		
85	<i>Cephalosporium</i> sp.									67	50	50	17	17		67	83	50	83		33	100	67	83	33	67	67	85	
24	<i>Aspergillus terreus</i>																			100	17	33						24	
8	<i>Penicillium funiculosum</i>		17			17	33	33		50	17	17	17	33		50	33	83	67	50	33	100	17	17		50	17	8	
86	<i>Cephalosporium</i> sp.					17			33	67			33		33	17	67	33	50	83		33						86	
35	<i>Thielavia basicola</i>		17										17					17		67	83							35	
11	<i>Penicillium roseo-purpureum</i>														67					67	67							11	
83	<i>Botrytis</i> sp.		67			33				17					50		17			67				17	50			83	
63	<i>Myrothecium striatissporum</i>																					67		50				63	
81	<i>Periconia</i> sp.									17	33	17		50		17		33	67		50					33		81	
27	<i>Aspergillus flavipes</i>									17						17				17	17		17	33	17	33	17	27	
40	<i>Chaetomium subterraneum</i>		33	17			33				17	17		17		33						67	33					40	
70	<i>Coniothyrium</i> sp.		17			17	17				50				17		50			17		17			67		50	70	
66	<i>Heterosporium terrestre</i>									17						33		17				17		50			33	66	
37	<i>Haplosporangium</i> sp.								17	33				17			17	33						67		17		37	
34	<i>Phoma conidiogena</i>		17																		33			17				34	
51	<i>Fusarium tricinatum</i>		17	17										17	33						17		17					51	
38	<i>Mortierella</i> sp.					17																17	17		17			38	
DRY PRAIRIES																													
20	<i>Spicaria violacea</i>			50			33	33	67	33	33	17	17	17	100	50	17	83	67	83	83	50	83	100	100	100	100	67	20
26	<i>Aspergillus fumigatus</i>				33				67	17			33	83	67	17	17	100			83	100	100	67	17	83	50	100	26
43	<i>Tilachlidium</i> sp.				33				17		100	17	50	33	67	83	33	83	17	83			83	50	50	50	67	100	43
58	<i>Myelia sterilia</i>		33	33	17	17	17	17		33	50	17	17	50	50	50	50	50	50	67	50	67		33	33	50	33	100	58
52	<i>Fusarium solani</i>		17	33	50	50	17		100	83	50	50	33	50	33	67	33	50			33	33	83	83	50	100	50	33	52
94	<i>Myelia sterilia</i>																									100	50	94	
89	<i>Dematiaceae</i> sp.					17				17		33				50				50	17	33	17			67	67	89	
82	<i>Cephalosporium</i> sp.															50	17			17			33	83		50	67	82	
48	<i>Cephalosporium</i> sp.					17			17					17		17				50			50		17		67	33	48
84	<i>Cephalosporium</i> sp.																				17					17		84	
71	<i>Pyrenochaeta</i> sp.			50																		17		50		33		33	71
12	<i>Penicillium megasporum</i>													17								17	17	17	17		33	12	
91	<i>Phialophora</i> sp.																									50		91	
21	<i>Scoptariopsis</i> sp.										17					17				17						33		21	
45	<i>Curvularia peniculata</i>										17					17				17		17			33			45	
25	<i>Aspergillus niger</i>												17					17			17				17		17	25	

TABLE IV. Number of species and special groups

Fungal group	CONTINUUM INTERVALS				
	100-180	180-260	260-340	340-420	420-500
Average no. of species/ prairie sampled	34.0	39.3	45.6	35.4	34.6
<i>Penicillia</i>					
No. of species	21	18	51	29	14
Ave. % of total	8.8	15.3	18.6	13.5	13.3
<i>Mucorales</i>					
No. of species	16	11	25	14	8
Ave. % of total	6.8	9.3	9.0	6.5	7.5
<i>Fusaria</i>					
No. of species	19	6	19	17	8
Ave. % of total	7.9	5.1	6.8	7.9	7.5
<i>Aspergilli</i>					
No. of species	4	3	9	14	8
Ave. % of total	1.6	2.5	3.3	6.5	7.5
Total no. of species per interval	238	118	277	215	106

(0.2-7.9 mil.) and for bacteria 1:32 (0.1-3.2 mil.) per gram of soil. The main source of error of mean counts, according to Rose and Miller, was due to variation in the sampling cores in the field, much less being due to subsampling and plating method in the laboratory.

However, our quantitative data did provide some indication of a pattern that was dependent on the soil environmental gradients of the prairie. A running average of three was employed as a statistical method of bringing to light the pattern, with the resultant calculation shown in Figure 7. An average of the calculations for each interval was superimposed on the running average. It indicates that the mesic prairies supported the highest populations of fungi per gram of dry weight of soil. This may have been due in part to the anaerobic conditions which prevailed in the wet prairies throughout at least a portion of each year. The thin soil, relatively low soil moisture content, extreme temperatures, and limited organic material were probably among the more important

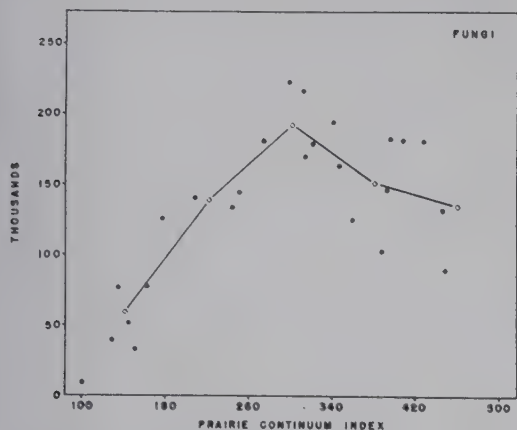


FIG. 7. The numbers of fungi per gram of dry soil (running average) along the prairie continuum. The line curve represents the average per interval.

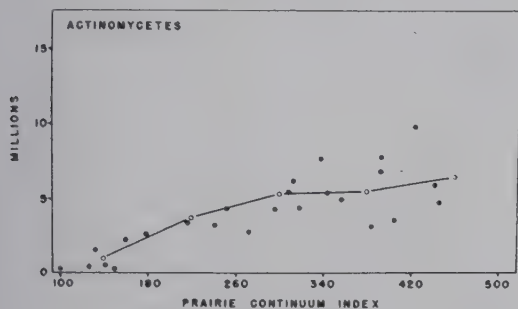


FIG. 8. The numbers of Actinomycetes per gram of dry soil for each stand along the prairie continuum. The line curve represents the average per interval.

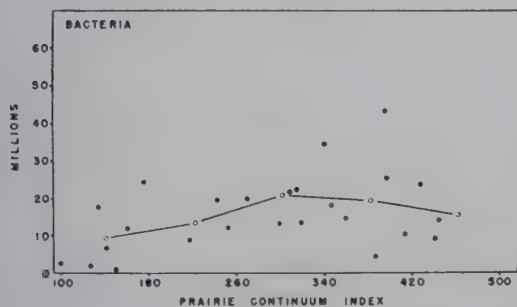


FIG. 9. The numbers of Bacteria per gram of dry soil for each stand along the prairie continuum. The line curve represents the average per interval.

factors which limited the numbers of soil fungi in the dry prairies.

The actinomycetes showed an increase in numbers towards the dry end of the gradient (Fig. 8). The curve on the graph represents an average of the recorded numerical counts of actinomycetes

in each stand for each interval. Not only was there a proportional increase, but also an actual increase in the numbers of organisms.

The bacteria exhibited only a small numerical crest in the mesic portion, dropping off towards both wet and dry prairie habitats. The graph (Fig. 9) represents an average of counts of bacteria for each stand according to intervals.

Without doubt the most notable change in environment from prairie to prairie was the extreme variation in soil moisture content. The wet prairie may have a water content well above field capacity during the spring while the dry prairie may be subjected to extremely high soil temperatures and very low moisture content during late summer and fall. These extremes were reflected to some extent in the numbers of microorganisms found in the habitats mentioned.

While soil moisture content may fluctuate from day to day, since it may be rapidly altered by the daily weather, it does tend to remain within certain limits in a particular soil. When the numbers of the fungi were plotted against soil moisture content, at the time of fungal sampling it became apparent that those prairies which had a moisture content of 20-40% supported the largest populations. The numbers of fungi dropped off rapidly in those soils with a high moisture content. This may be attributed to the anaerobic conditions in the water-logged soils.

Similar distribution curves were obtained for the actinomycetes and for the bacteria. As for the fungi, those soils with the intermediate amounts of soil moisture were apparently best suited for the support of large populations. A comparison of the distributions of numbers of bacteria and of actinomycetes indicated that the bacteria had a broader tolerance for moisture content than did the actinomycetes. The actinomycetes crested sharply at 25-35% moisture content then dropped off sharply towards the high moisture sites and somewhat less sharply toward the drier sites. The bacteria showed more range in numbers and a broader crest between 20-40% moisture content.

It is suggested that low organic matter content of the soil or higher temperatures may have become important controlling factors in determining the numbers of microorganisms in the drier sites rather than the mere lack of moisture. Very likely the anaerobic conditions of the wetter sites influenced the numbers of microorganisms. Anaerobic forms would not be expected to show up on the type of plates used in the present study. In a study of the higher vegetation of prairie stands Curtis (1955) found there was a close correlation between the species composition of higher plants

and the water retaining capacity for the wetter sites. The dry sites, however, were apparently independent of this factor. It was suggested that the soil depth was the important factor in this case.

DISCUSSION

The survey nature of the investigation under consideration here was in keeping with the general character of a series of investigations dealing with the ecological relationships between the soil microorganisms and the higher plant communities of Wisconsin. The present study is among the first to use methods of analysis commonly applied as a means of determining the ecological relationships of higher plants in the examination of ecological aspects of microorganisms. To establish relationships between the soil microflora and the higher vegetation twenty-five prairie stands have been analyzed. The selection of the stands was aided by the previous works of Curtis and Greene (1950) and Curtis (1955) in which the habitats were clearly defined and the affinities of the higher vegetation were established.

Prairie stands were carefully chosen with the express purpose of providing a substantial framework of microfungi distributional ranges. It was essential that these prairies be relatively undisturbed so that the "normal" or "typical" fungal populations could be recognized as they occurred along the environmental gradients of the prairie. Thus, the value of future, more detailed studies of particular habitats would be enhanced as they were related to the already existing framework.

The use of relative frequency as an analytical device, as in ecological studies of higher plant vegetation, has brought to light general principles concerning the distributional ranges of the prairie soil microfungi of the region studied. Analogous with the situation demonstrated for the higher vegetation, species constituents of the fungal communities continuously changed from habitat to habitat along the prairie landform gradients. A majority of the forms possessed amplitudes of environmental tolerance which permitted them to grow in habitats ranging over a large portion of the gradient, although most of these did exhibit a preference for the environmental conditions of a particular type of prairie. This situation contrasts with that reported by Tresner, et al. (1954) for the distribution of fungi in the soils of the southern Wisconsin hardwood forests in that considerably fewer of the forest fungi exhibited such broad amplitudes. As previously noted, about one fourth of the species of prairie soil fungi dealt with were found in only a limited portion of the continuum. If they occurred elsewhere, it was at such low frequency that they did not show up with

the sampling and isolation procedures employed. Forest fungi with distributional patterns of this type were termed "indicator species" by Tresner. However, Tresner's "indicators" exhibited high frequencies, while almost all of the prairie forms of limited range had low frequencies. Thus, it does not seem wise at this point to use the term "indicator" in connection with any of these prairie forms, although further studies may later justify this step. It is perhaps not without significance, for instance, that a new species of *Emericellopsis* was isolated 109 times from four low wet prairies but was not found at all in any of the four higher prairie intervals and, furthermore, has apparently never before been encountered by mycologists in any situation.

There have been two main schools of thought, among mycologists, in respect to the character of the soil microfungi flora. The one school has maintained that distribution of species is more or less haphazard or without pattern, while the second school has contended that there are, in fact, differences evident from location to location depending on the soil environment. Probably a majority of modern mycologists have tended to hold to the latter view without, however, having strong basis for their position, for good studies bearing on the question have been very few and there have been conflicting reports. Only very recently has this situation begun to improve. Warcup (1951) found that while very few of the fungi isolated from five grassland soils of England were confined to a single soil type, there were two groups of fungi evident: those which preferred the acid soils and those which preferred the alkaline soils. It was his conclusion that soil fungi live in ecological communities which are governed by factors such as soil type. Although the soil types were correlated with pH, Warcup considered the role of pH as of uncertain importance in the distribution of fungi. Stenton (1953) in an analysis of soils from two sites in a marsh concluded that the differences between the fungal floras of the two sites were quantitative rather than qualitative. Saito (1952) likewise had demonstrated that there were quantitative changes in the microfungi flora from habitat to habitat. The conclusion of Tresner, et al. (1954) that there is a series of progressively changing species combinations along the gradient of the upland-hardwood forest continuum of southern Wisconsin and the similar conclusion of the present investigation in respect to the soil microfungi of the prairies in Wisconsin would seem to add considerable weight to the concept of distinctive microfungi floras in the soils of various vegetational areas.

One of the very striking contrasts in the fungal populations of the hardwood forest soils and prairie soils of this state, as brought out by the studies of Tresner, et al. and the writers, is found in connection with the genera *Fusarium* and *Aspergillus*. Whereas *Fusaria* were encountered only infrequently in the forest soils, they are among the most prominent and characteristic members of the prairie soil flora. *Aspergilli* were found to be even less common than *Fusaria* in the forest soils studied by Tresner. Indeed, so seldom was *Aspergillus* encountered on Tresner's isolation plates that it was catalogued as a "rare" form. (Interestingly enough, two of the very few *Aspergillus* isolates which Tresner did obtain were found to represent a new and exceptionally interesting species (Raper, et al. 1953). On the other hand *Aspergilli* (esp. *A. fumigatus*) were found to be common in prairie soils.

The relationship between the higher plant cover of the Wisconsin prairies and the microbial populations of the soils of these prairies is a matter of considerable interest. It is now clear that there is at least some general sort of correlation between the two, for shifts in the higher plant populations along the continuum gradient are paralleled by similar shifts in the fungal and bacterial populations, and distributional patterns of individual fungal species have been found to be remarkably similar to the distributional patterns of higher plant species. The reasons for these parallelisms are unfortunately not yet clear. It is probably safe to assume, however, that any influence which the higher plant vegetation is exerting on the microbial populations is indirect. Undoubtedly the character of root systems, the character of higher plant remains, etc. contribute to differences in the character of the soil environment from habitat to habitat—differences to which the fungi and bacteria respond. But this is almost certainly only one of a complex of factors influencing microbial distribution. Of the various factors contributing to the soil environment, it would appear that soil moisture content may be one of the most important as far as distribution of microorganisms is concerned. Such a soil factor may exert a direct conditioning influence on both the higher plant cover and the microbial populations.

It is concluded from the present study that the soil microfungi of the Wisconsin prairies do not form discrete communities in which particular forms are consistently associated; rather there appears to be a series of continuously changing combinations of fungal species along the prairie continuum. This situation parallels the distribution of the microfungi of the hardwood forest and

the higher plant vegetation of both prairies and hardwood forests of the same geographical region.

SUMMARY

1. The soil microflora of twenty-five prairies in Wisconsin was studied by a uniform isolation method. The prairies represented the full range of topographic types, from very wet to very dry. They were located in 12 Wisconsin counties in the south and central portions of the State.

2. When the stands were arranged in a gradient based on their changing complement of higher plants, it was found that the soil fungi paralleled the behavior of the higher forms. Some species were ubiquitous in that they occurred in all prairies, some species showed a definite optimum in a definite portion of the gradient, while more than one-quarter of the species were restricted to a limited segment of the gradient.

3. The total number of species of soil fungi reached a maximum in the mesic prairie stands. This was also true of the species in the genus *Penicillium*. On the other hand, the *Aspergilli* were definitely more prevalent in the dry prairies while the *Mucorales* tended to do better in the wetter sites. The genus *Emericellopsis* was restricted to the wet prairies. In terms of number of individuals, the greatest population of fungi and bacteria occurred in mesic sites, while the actinomycetes were most numerous in the dry prairies.

4. The fungal species did not form discrete communities in which particular forms were constantly associated but appeared to be arranged in a continuum of the same type as that shown by the higher plants.

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A PHYTOSOCIOLOGICAL ORDINATION OF THE CONIFER SWAMPS OF WISCONSIN

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INTRODUCTION

This paper is the result of a study of 106 conifer swamps in Wisconsin. The conifer swamp is here defined as an area in which conifers over four inches diameter breast height are the dominant trees; the water level is not above the soil surface throughout the year, but is always near the surface; the soil is obviously high in organic matter, but is not necessarily peat; the soil is either well or poorly aerated; and the water running or stagnant.

Those conifer swamps whose soils are poorly aerated, poorly drained, and peaty, and whose ground vegetation is dominated by ericads, are called conifer bogs. Bogs have long been a popular study area for botanists, and the literature is voluminous. Among the more recent papers from areas near Wisconsin are those of Conway (1949) and Gates (1942).

The author wishes to thank Dr. J. T. Curtis for advice and constructive criticism during the preparation of this paper, Dr. Grant Cottam for advice on field methods, Dr. S. A. Wilde and Dr. G. K. Voigt for advice in soils problems, and Mr. James Zimmerman for the identification of all Carices. This study was made partly during the tenure of a Wisconsin Alumni Research Foundation Fellowship and partly during the tenure of a National Science Foundation Fellowship, for which the writer is deeply appreciative.

METHODS

Choice of stands

The heaviest concentration of conifer swamps remaining in Wisconsin is in the northern part of the state where there are large forested areas, and where modification by draining, agriculture and cattle grazing is comparatively slight. Severe deer browse damage, while present, tends to be limited to deer yards (Christensen 1954). Data collection was concentrated in this northern region, particularly around the University of Wisconsin Biological Station in Vilas County.

Surveyors' records show that there were formerly extensive areas of conifer swamp in southern Wisconsin. Remnants of these exist today, more or less disturbed by agriculture, cattle grazing, fire and drainage. In view of the tension

zone between vegetation of northeastern Wisconsin and vegetation of southwestern Wisconsin, as described by Brown and Curtis (1952) and Curtis and McIntosh (1951), it was decided that a comparison of some of these remnants with the less disturbed northern Wisconsin conifer swamps would be interesting. Data from ninety conifer swamps in Wisconsin north of the tension zone (here called northern swamps) are treated, and data from sixteen conifer swamps in Wisconsin south of the tension zone (here called southern swamps) are treated separately for the purpose of comparison.

No conifer swamps from the Driftless Area are included, since none are known to exist intact today. Hansen (1933) discussed those stands available at that time.

Location of stands, approximate center of tension zone, and Driftless Area are shown in Figure 1.

Location of Stands



FIG. 1. Map of Wisconsin on which small circles indicate location of stands, the solid line represents the approximate middle of the tension zone, and the dotted line marks the Wisconsin borders of the Driftless Area.

In far north-central Wisconsin, swamps are so plentiful that they are easily found by reconnaissance in automobile or on foot. In localities where swamps are less common, stands were located by inspection of soil maps, quadrangle maps, aerial photographs, and by talking with persons familiar with the area. Once potential stands for study were located, they were visited, and included in the study only if the above mentioned criteria of a conifer swamp were satisfied, if free of severe recent disturbance, and if apparently homogeneous in tree cover.

Tree data methods

Tree species and basal areas were determined by the tree-centered quarter method (Cottam, Curtis, and Hale 1953), while distances between trees were measured by the wandering quarter method (Catana 1955). In the method used, the species and diameter breast height of five trees at each point are recorded (the central tree and the nearest tree in each of the four quadrants centering on this tree). The distance from the central tree to the nearest tree within the 90° angle bisected by the direction of traverse is measured, and from the latter tree to its nearest tree, and from this tree to its nearest tree, always with a 90° angle of inclusion. The last tree becomes the center of the second point. One hundred trees and sixty distances (twenty points with three distances after each point) were recorded for each stand.

This method permits each point to be located objectively and results in a larger sample than the random pairs method (Cottam and Curtis 1949), where a tally of twenty points would result in data for forty trees and twenty distances.

Saplings were generally few under the canopy of swamp conifers, and no sampling technic was devised for them, other than to note the few cases where they were numerous.

Herb data methods

Herbs and other non-tree species were sampled by twenty quadrats one meter on a side, spaced a predetermined number of paces apart, usually ten paces or roughly fifty feet. The quadrat line was laid along the tree traverse in order to minimize differences in environment of the samples, and presence of herbs within each quadrat was recorded. This quadrat size gave very high frequencies for a few plentiful species such as *Chamaedaphne*; a slight reduction in quadrat size would have given more meaningful data for these species. Before the quadrat data were gathered, a reconnaissance walk was made, and all species seen were recorded. This provided presence data

on species too rare to occur in the quadrats. Mosses were not recorded. Plants of uncertain identity were collected, and the identity of forbs and grasses verified in the laboratory by the author. Carices were identified by Mr. James Zimmerman of the University of Wisconsin Botany Department. Specimens are on file in the University of Wisconsin herbarium. Nomenclature follows that of Gray's Manual of Botany (Fernald 1950).

Physical environmental data

A composite soil sample was taken, composed of four sub-samples each of about 125 cu. cm. of soil, usually gathered in the 5th, 10th, 15th, and 20th quadrats. During the first year's field work, samples were collected only from the upper soil layer (in the case of *Sphagnum* or *Carex* peat this was interpreted as the layer immediately below the last green layer of organic matter). During the second year samples were taken also from the three foot depth, or in some cases, shallower depths when sand or marl were encountered above three feet. During the second year both surface and lower samples were taken in duplicate.

The relation of the dry weight of a sample to its original wet weight was used to estimate the total dry weight of the duplicate. The duplicate, shortly after collection, was mixed with a large amount of water and sieved, resulting in a fraction whose particles could not pass through a five mm. sieve (the coarse fraction), and a fraction whose particles passed through a 5 mm. sieve but not a 1 mm. sieve (the medium fraction). The difference between the sum of the weights of the dried coarse and medium fractions, and the estimated total dry weight was accepted as the weight of the particles which passed through the 1 mm. sieve (the fine fraction). Fraction weights were expressed as percentages of the total weight. This method was suggested by the technic described in Conway (1949).

Further tests were performed on the samples dried in total. They were ground, and passed through a 2 mm. sieve. The water holding capacity, calcium, magnesium, nitrate, ammonium, phosphorus and potassium content, and the pH were determined with the resulting soil powders. Water holding capacity was determined by the standard procedure using Hilgard cups. Results given are the weight of water held expressed as a percentage of the weight of the dry soil. Content of available mineral nutrients was determined by the University of Wisconsin Soils Laboratory, and is expressed in pounds per acre per seven inches depth, here abbreviated to ppa. The pH measurements were made on a Beckman pH

meter using water suspensions of the powdered soil which had settled overnight.

Tests for presence of ferrous and ferric ions were performed in the field, according to the method mentioned in Pearsall (1938). Small quantities of soil were mixed with an alcoholic solution of potassium thiocyanate. Pink color indicates presence of ferric ion. If a small amount of hydrochloric acid is added to a negative or a faint ferric result, occurrence of, or deepening of pink color indicates presence of ferrous ion which has been oxidized to ferric ion by HCl. Presence of ferrous rather than ferric ion indicates reducing conditions.

Catalytic capacity of the soil was determined according to the method of Wilde and Mikola (1951). Approximately one half teaspoonful of soil is mixed with 5 ml. of 5% hydrogen peroxide in a closed chamber, and the pressure of the oxygen given off by the action of the soil on the hydrogen peroxide is measured with a manometer. The evolution of oxygen is thought to be due to enzymes of aerobic bacteria in the soil, or to the presence of manganese. Thus, in the absence of manganese, the tests may furnish an indication of soil aeration. Figures here recorded are the number of mm. pressure built up in two minutes. Measurements were made on the surface and on the three foot deep layer.

Sunlight is roughly indicated by an estimate of the average percent tree cover. This was purely a visual estimate and any given measure has value only in relation to other values. All estimates were made by the author.

Vegetational and environmental data are on file in the University of Wisconsin Plant Ecology Laboratories.

ANALYSIS OF DATA

Tree data

Density, frequency, and dominance (basal area at breast height) were calculated for each tree species. The density of each species was divided by the sum of densities in the sample, giving the relative density, or the percent of the sum density. The same procedure was followed for frequency and dominance, giving relative frequency and relative dominance. The sum of the three relative values for each species is called the importance value (IV) for that species. The method is further discussed in Curtis and McIntosh (1951).

Herb data

Frequency and relative frequency were calculated from the herb quadrat records. Total number of herb species in each stand was obtained by

adding the number of herbs appearing in quadrats to those appearing only on the presence lists. Mean frequency of herbs was calculated by dividing the sum frequency in a stand by the total number of herb species appearing in its quadrats.

Method of ordering of stands

One method of studying the data of many stands is to place the stands in some logical order and search for patterns of environmental factors of vegetational compositions in relation to this order. Ordering on the basis of an environmental factor requires the assumption that the chosen factor is one of the most, if not the most, important of the factors. Since the importance, and the interrelations of the factors are not all known, and since it is possible that some of the factors may be unknown, the stands were ordered on the basis of the resultant of all these vectors. That resultant is the vegetation, the measurable expression of the many environmental conditions.

A preliminary attempt was made to order the stands by the strip method of Curtis and McIntosh (1951). The method proved difficult to apply to the large number of species of herbs, and when tried with the tree data alone, results were poor due to the paucity of tree species with high importance values. There are only four tree species which attain values of any significance: *Larix laricina*, *Picea mariana*, *Thuja occidentalis*, and *Abies balsamea*. With such uniform tree composition it was difficult to accomplish ordination based on the trees only.

The stands therefore were ordered according to similarity of herb vegetation as measured by a coefficient of community here called W. This coefficient is a modification of that of Gleason (1920) and differs from that used by Sørensen (1948) in that frequency data rather than presence data are used. The formula may thus be stated as follows:

$$C = \frac{2W}{a + b} \times 100$$

Where C = coefficient of community

a = sum of relative frequencies of Stand 1

b = sum of relative frequencies of Stand 2

W = the sum of the lower relative frequencies for each species in the two stands. If a species occurs in only one of the two stands, its lower relative frequency is of course zero.

The quotient is multiplied by 100 to raise the C values to whole numbers.

Since relative frequency is used, $a + b$ is 200 in all cases. Thus the formula becomes

$$C = \frac{2W}{200} \times 100$$

which simplifies to $C = W$. A W value of 100 indicates identical stands; a W value near zero indicates stands with very little similarity.

When all stands were compared with all other stands, it was found that the stands could not all be placed in a manner consistent with all the W values unless even more than three dimensions were utilized. Because of the difficulties of accomplishing such arrangements, a method developed and discussed by Bray (1955) was used as follows.

A table of W values for a single stand compared to all other stands was compiled. This reference stand was chosen subjectively as representing a vegetational extreme among the stands studied. The stand least similar to this reference stand was then compared with all other stands. Thus two reference points, each with its table of values, were set up. Since the two reference points are highly dissimilar, they may be considered as opposite end points of a gradient. The position of the other stands along this gradient were estimated by the following formula of Bray:

$$X = \frac{IW + CRW}{2}$$

Where X = the position of a given stand on the gradient

IW = the W value of this given stand with Reference Stand 2

CRW = the largest W value of the two tables, minus RW

RW = the W value of the given stand with Reference Stand 1

The difficulties of such an attempt to compress a multidimensional figure into one dimension are apparent. It is possible that the compression is irregular or that the index is not a true measure of similarity. Even if the index were a true measure, and stands were well arranged in a multidimensional figure, each point would be located within a sphere of uncertainty, since the same stand, if re-sampled, would give slightly different results. As yet, a method to avoid these difficulties has not been developed.

Ordering of the northern stands

As explained above, the northern stands were treated separately from the southern stands. Stand 21 was chosen from among the ninety northern swamps since it was extreme in type, being a kettle hole bog with high quantities of *Picea*

mariana, *Ledum groenlandicum* and other bog plants. Herb composition of each of the 89 other stands was compared to Stand 21 and W values obtained. The stand most similar to Stand 21 had a W value of 85 with it. Stand 71 had the lowest W value above zero with Stand 21; it was chosen as the second reference point and herb composition of all stands were compared with it.

The stands were arranged along the gradient between Stand 21 and Stand 71 by the method described above. The gradient was then divided into segments of ten units each. Segment 9 contained only two stands, and was combined with Segment 8. X values included in each gradient segment are as follows:

Segment	1	X values	1 through 10	21 stands
2	11	20	21	
3	21	30	4	
4	31	40	3	
5	41	50	4	
6	51	60	6	
7	61	70	14	
8	71	84	17	

Behavior of species in northern stands

The average importance values of the tree species within each segment appear in Table I. To the left of the gradient *Larix laricina* and *Picea mariana* dominate; to the right *Thuja occidentalis* and *Abies balsamea*. Trees of lesser importance are *Pinus banksiana*, *P. resinosa*, and *P. strobus* to the left; and to the right *Acer rubrum*, *Betula lutea*, *Fraxinus nigra*, *Picea glauca*, *Populus balsamifera*, and *Tsuga canadensis*. *Pyrus americana*, *Ulmus americana*, and *Betula papyrifera* were present in very low amounts to the right. *Populus tremuloides* is found throughout the gradient. This is similar to the ordering of the tree species found by Christensen (1954).

Figure 2 is a composite graph of most of those

TABLE I. Importance values of tree species averaged within each segment of the gradient of northern swamps

Segment	1	2	3	4	5	6	7	8
<i>Larix laricina</i>	78	58	87	21	102	37	11	5
<i>Picea mariana</i>	196	183	184	243	83	79	34	6
<i>Pinus banksiana</i>	16	29	1	...	...	...	...	...
<i>P. resinosa</i>	2	...	2	...	4	...	...	...
<i>P. strobus</i>	5	6	21	1	6	...	1	...
<i>Populus tremuloides</i>	2	2	3	...	...	6	1	4
<i>Abies balsamea</i>	...	1	1	18	35	63	158	106
<i>Thuja occidentalis</i>	...	4	...	2	71	76	143	139
<i>Fraxinus nigra</i>	...	...	...	...	...	30	11	5
<i>Acer rubrum</i>	...	...	...	3	...	...	2	2
<i>Betula lutea</i>	...	...	...	...	...	6	8	25
<i>Picea glauca</i>	...	...	...	1	...	...	1	3
<i>Populus balsamifera</i>	...	...	...	...	...	...	...	5
<i>Tsuga canadensis</i>	...	...	...	9	...	...	4	3

species which were not infrequent. The abscissa is divided into the above explained segments, and the ordinate represents importance value of tree species, frequency of Carices, and relative frequency of all other plants. Figure 3 illustrates the behavior of four typical species.

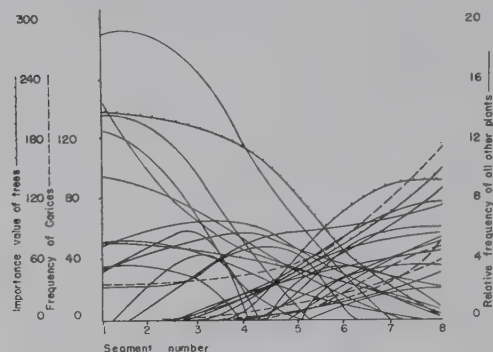


FIG. 2. Composite graph of behavior of species found in Wisconsin conifer swamps. The abscissa numbers represent categories (segments) into which stands were classified according to similarity. Ordinate represents importance values of trees, frequency of carices, and relative frequency of all other plants.

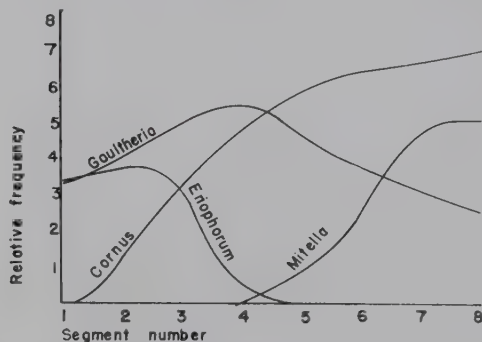


FIG. 3. Relative frequency of four species from Figure 2 which peak in different categories (segments). Species are *Cornus canadensis*, *Gaultheria hispida*, *Eriophorum virginicum*, and *Mitella nuda*.

Non-tree species which peak in, and are limited to the left, are: *Eriophorum spissum*, *Chamaedaphne calyculata*, and *Carex lasiocarpa*. Species also peaking to the left but extending somewhat farther to the right include: *Eriophorum virginicum*, *Andromeda glaucophylla*, *Kalmia polifolia*, *Vaccinium angustifolium*, *V. oxycoccus*, *Ledum groenlandicum*, and *Vaccinium myrtilloides*. *Gaultheria hispida* and *Gaultheria procumbens* peak in the center. *Rubus pubescens* peaks slightly to the right of the center and drops out completely to the left. *Carex trisperma* peaks

to the right; its amplitude extends throughout the gradient. Non-tree species which peak to the right but extend for varying distances to the left include: *Coptis groenlandica*, *Cornus canadensis*, *Trientalis borealis*, *Clintonia borealis*, *Linnaea borealis*, *Pyrola secunda*, *Carex disperma*, and *Galium triflorum*.

Species limited to the right hand end of the gradient include: *Viola pallens*, *Mitella nuda*, *Dryopteris spinulosa*, *Dryopteris disjuncta*, *Aster macrocarpa*, and *Aralia nudicaulis*.

Correlation of environmental factors

Mineral content of the surface soil is strikingly correlated with the gradient. Calcium, magnesium, potassium and phosphorus contents of the surface soil increase sharply toward the right, calcium from 1000 pounds per acre to 8000 ppa, magnesium from 150 ppa to 700 ppa, potassium from 200 ppa to 500 ppa, and phosphorus from 30 ppa to 70 ppa. The tests used to determine mineral content utilized a dilute acid, and therefore probably give a rough estimate of the minerals available to the plants; ions held by the sphagnum probably would not be measured.

Catalytic capacity of the surface soil, as measured after two minutes reaction with 5% hydrogen peroxide, increased from 20 mm. at the left to 80 mm. at the right, probably indicating increased aeration of soil. Incidence of ferrous ion decreased to the right, also reflecting increased aeration.

Water holding capacity at the surface decreased from 850% at the left to 500% at the right, a corollary of decreasing sphagnum peat.

The pH of both upper and lower layers showed only a slight increase toward the right, remaining near 4.5; those pH values lower than 4.0 occurred near the left end of the gradient. The pH values were determined on dried and ground soils, and do not represent field conditions directly.

Ammonium ion of the surface soil peaked slightly in the center of the gradient at 80 ppa and sloped to 40 ppa at the left and 45 ppa at the right.

The proportion by weight of the coarse fraction of the surface soil showed a sharp drop from 70% at the left of the gradient to 50% at the far right. The proportion of the medium soil fraction remains approximately the same from left to right, at 25%, while the proportion of fine soil fraction rises sharply from 15% at the left to 45% at the center, and is uncertain in trend to the right.

There is no clear correlation of any of the three foot depth measurements with the gradient, except for the three foot depth determination of calcium, which rises from 1000 ppa at the left to 10,000 ppa at the right, and of potassium which drops

from 250 ppa to 100 ppa at the right. This lack of correlation is not surprising, since different layers of a swamp may have been laid down by entirely different types of vegetation during its historical development.

Percent cover, and therefore intensity of shading, increased from about 20% on the left to about 65% on the right. Behavior of four of these habitat factors is illustrated in Figure 4.

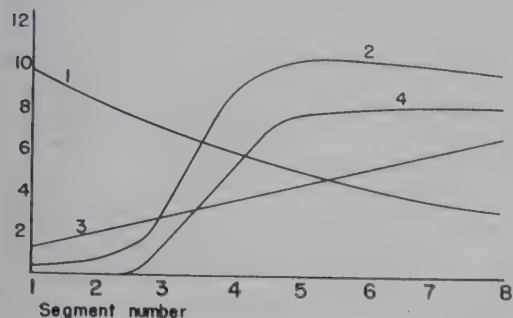


FIG. 4. Behavior of four habitat factors in relation to the gradient. 1: Water holding capacity of surface soil (10=1000%). 2: Calcium content at three foot depth (10=10,000 ppa). 3: % cover (10=100%). 4: Calcium content of surface soil (10=10,000 ppa).

Correlation of phytosociological trends

The total number of non-tree species present increases from 11 at the left to 33 at the right; the number of species present in quadrats and the number recorded as present during the reconnaissance walk increase in the same direction. The proportion between those species present in the stand but not occurring in quadrats and the total number of species, as expressed by a percent, showed a slight decrease from 40% at the left to 30% at the right. The curve showing mean frequency remains approximately level at about 30 from left to right, although it is at its highest in Segment 1 where the total number of species is lowest.

Mean basal area increased from ca. 20 sq. in. on the left to ca. 37 sq. in. on the right. This is related to the increase in percent cover.

Ordering of the southern stands

Data from sixteen stands south of the tension zone were collected. These stands were arranged along a gradient of decreasing similarity to the northern spruce-tamarack bog by Bray's method, the same method that was used for the northern stands. Since there were so few southern stands, it was possible to perform a check on the arrangement. A complete matrix of values of W was compiled, showing the relation of each stand to every other stand, and the stands arranged in the

TABLE II. Complete matrix of W values (a similarity index) for the southern swamps arranged so that mutually similar swamps are grouped together. Figures on the ordinate and abscissa are stand numbers; all other figures are W values

[illegible]

order obtained by Bray's method (Table II). When such a matrix is well arranged, with the most similar stands placed next to each other, high *W* values fall on the hypotenuse. This matrix appears to be reasonably well arranged, and we may assume that the gradient resembles the actual rank of similarities. No two southern stands attain the high degree of similarity found between some northern stands.

Behavior of species of southern swamps

The gradient of southern swamps was divided into four segments of ten units each, containing two, two, four, and eight stands. The relative frequencies of each non-tree species, and the importance values of each species of tree were averaged within these segments. The sample is too small to do more than indicate trends.

Larix laricina remains high throughout the gradient, *Picea mariana* and *Pinus strobus* decrease from left to right. *Thuja occidentalis*, *Betula papyrifera*, *Ulmus americana*, *Populus tremuloides*, *Acer rubrum*, and *Fraxinus nigra* enter toward the right; these are found in the right hand end of the northern gradient.

Non-tree species which peak at the left hand extremity of the southern gradient, or that end more similar to the northern conifer bogs are: *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Vaccinium oxycoccus*, and *Andromeda glaucophylla*. These species are all typical of the left hand, or *Picea-Larix* end of the northern gradient.

Non-tree species which peak in the middle of the southern gradient are *Trientalis borealis*, *Rhus vernix*, and *Gaylussacia baccata*. *Trientalis* is abundant in northern swamps of the right hand end of the northern gradient.

The right hand end of the southern gradient contains those stands which least resemble the northern spruce-tamarack swamps. Here are peaked *Viola pallens*, *Solidago gigantea*, *Scutellaria epilobifolia*, *Rubus pubescens*, *Maianthemum canadense*, *Lysimachia terrestris*, *Dryopteris thelypteris*, *Cornus stolonifera*, and *Aster junciformis*. Most of these are not found in northern conifer swamps, but *Viola pallens*, *Rubus pubescens*, and *Maianthemum canadense* are abundant in swamps to the right hand, or cedar end of the northern swamp gradient.

Environmental and phytosociological data of southern swamps

Surface nutrients and pH increase, while the water-holding capacity decreases, toward the right of the gradient. Ferrous and ferric ion tests are negative in all stands tested. There is a decrease in the mean frequency concomitant with an increase in the number of species from left to right.

DISCUSSION

This ordering of stands is on the basis of community resemblances at one point in time; it is not intended to illustrate development of one community throughout a period of time. Since the vegetation of a stand at a given time closely resembles its immediately previous and immediately following vegetation, if development is undisturbed, and since the stands included were in various stages of development, the ordering unavoidably parallels the developmental pattern in general.

The trees of the northern swamps show a high correlation with the ordering of stands on the basis of herb layer. This is to be expected since trees are influenced by many of the factors which influence the herb layer, and because the trees themselves influence the herb layer. Thus there are two extreme types of conifer swamp in Wisconsin: the spruce-tamarack type and the cedar-balsam type.

Certain curves of species amplitude taper across the central area of the northern swamp gradient, and the curves of two species peak there, indicating that the extreme types are not distinct, but are related by intermediate types. On the other hand, the number of intermediately-peaking species is small, and the number of intermediate stands is also small; segments 4 through 6 contain only 13 of the 90 stands. On the basis of these data alone, there is some justification for drawing an arbitrary line between the two community types.

No such abrupt vegetational change is indicated in the southern stands, and more species peak in

the intermediate stands. Cedar plays a very small role in these southern swamps and the tree composition of most southern swamps grades from tamarack (or black spruce near the tension zone) to upland species.

The status of intermediate stands is clarified by noting the reproduction and spreading habits of cedar.

Cedar may spread naturally either by seeding or by layering. The latter occurs when low branches touch the soil and send out roots and stems. The young plant may be separated from the old tree by death of the connecting branch, or may remain connected, probably deriving nutrients and water from the old tree. The latter condition would enable cedar to invade somewhat unfavorable areas.

Maki (1931) reported that the type of cedar reproduction which will occur depends on the seedbed. In cedar swamps with open, sphagnum-free floors, the young trees are usually seedlings; in dense sphagnum, layering is favored, and seedlings may be precluded.

This and observation from the present study indicate that cedar often enters adjacent spruce or tamarack stands by layering. Changes in environment correlated with cedar invasion prevent the growth of spruce and tamarack seedlings and many associated non-tree species. Thus the advancing wall of vegetatively reproducing cedar eliminates these plants and causes a sharp transition zone. Sampling within this zone is unlikely because of its narrowness; sampling across it will be avoided as non-homogeneous.

The author has observed that when individual cedars have become established in a sphagnum swamp, probably by seeding into isolated favorable spots, they have spread by layering, and clumps of cedar within spruce or tamarack swamps result.

Cedar apparently does not enter dense spruce or spruce-tamarack swamps unless in a position to do so by layering; nor has the author observed many small tamarack or spruce trees in such stands when the lower branches of the old trees were too high for layering. Apparently these stands can exist for many years in a relatively static condition until the old trees burn, are wind-thrown, or die otherwise, at which time cedar may seed in.

If the death of the old trees is caused by fire, and is followed by an in-seeding of cedar, an intermediate understory cannot be expected by the time the cedars have reached 4 inches DBH. Swamps where the old spruce trees are dying or are being wind-thrown in spots are uncommon in northern

Wisconsin, perhaps due to the forest fires which were frequent in the past, and which prevented the spruces from attaining old age. Figure 5 is a diagram of a two yard wide and 120 yard long transect through a handsome example of this infrequent type. The end of the transect enters a pure spruce bog. Such a stand visited when the cedar had just invaded would have been disregarded on the grounds that there were not enough trees over four inches DBH.

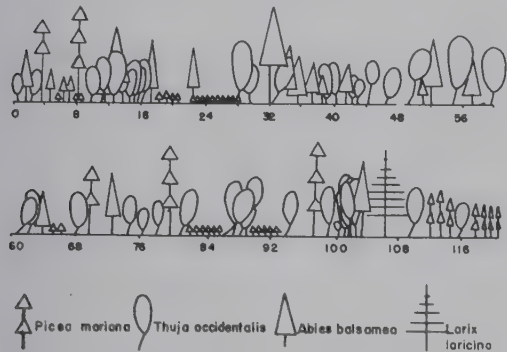


FIG. 5. Diagram of a two yard wide and 120 yard long transect through a conifer swamp intermediate between the spruce-tamarack and cedar-balsam types.

Stands of young cedar in easily accessible places are often cut to satisfy the high demand for cedar poles.

From the above discussion it is apparent that the paucity of data from swamps intermediate between the extremes of the spruce-tamarack type and the cedar-balsam type is due to: 1) Low number of intermediate stands in proportion to the number of extreme stands. This is partly explained by the apparent rapidity of the change from one extreme to the other, and the relative stability of stands of the extreme types. Intermediate stands are lacking when the transition is accomplished by the intervention of fire, and are destroyed by the lumbering of young cedars. 2) Omission of existing intermediate stands from the sampling data. This is explained by the narrowness of some intermediate stands, the non-homogeneity of others when sampled on a small scale, and the small number of trees of four inches DBH in still others.

SUMMARY

This paper is the result of a study of 106 conifer swamps in Wisconsin. A conifer swamp is defined as a forest stand in highly organic, wet to moist substratum with numerous conifers present; only stands in which the dominant layer of trees

is over four inches diameter breast height are included. Ninety of the stands are located north, and sixteen south, of a vegetational tension zone in Wisconsin.

Tree data were gathered by the tree-centered quarter method; 100 trees were recorded in each stand. Herb data were gathered by twenty quadrats of one meter on a side laid along the tree transect. Soil analyses and cover estimates were made.

Stands were ordered along a gradient based on the similarity of herb composition. Vegetational and environmental factors are correlated with this gradient. The extremes of the gradient represent the spruce-tamarack type and the cedar-balsam type of swamp. Species behavior indicates that these types are fairly distinct, but are linked by rather infrequent intermediate types. The status of these intermediate types is discussed.

Data from sixteen conifer swamps south of the tension zone are compared with the northern swamp data.

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SOME SILVICULTURAL CHARACTERISTICS OF WESTERN REDCEDAR IN SOUTHEAST ALASKA

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Recent studies by the Alaska Forest Research Center, designed to investigate the silvicultural characteristics of western redcedar (*Thuja plicata* D. Donn), have provided clues to the occurrence and behavior of this species in both old-growth and young-growth stands. Redcedar appears to react somewhat differently to its environment in the coastal forests of Southeast Alaska than elsewhere. It displays some silvicultural characteristics in this region which have not been reported.

In Alaska, redcedar is a major commercial species throughout its range (Fig. 1). It occurs at lower elevations in association with western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carr), and occasionally mountain hemlock (*Tsuga mertensiana* (Bong.) Carr) and Alaska cedar (*Chamaecyparis*

nootkatensis (D. Donn) Spach). From general observation redcedar appears to occur most abundantly on poor sites, often predominating on imperfectly drained soils or on rocky slopes where soil development is limited.

Cruise data from old-growth stands revealed that redcedar seldom occurred in smaller diameter classes although it often existed, or even predominated, in the larger diameters. Diameter distribution curves usually showed the greatest number of stems in the mid-diameter classes; a situation most typical of even-aged distribution. Western and mountain hemlock, however, displayed J-shaped curves typical of all-aged stands. Redcedar did not appear to be reproducing itself as did hemlock in well-stocked stands. These preliminary findings resulted in the following study designed to investigate more thoroughly the occurrence of redcedar in both old- and young-growth stands.

METHODS

Six sampling units were located in well-stocked old-growth cedar-hemlock types, dispersed over the range of redcedar in Alaska. Each unit consisted of a transect 10 chains long and 1 chain wide on which all live stems 5 inches d.b.h. and larger were recorded. In addition, live saplings (1.0 inch through 4.9 inches d.b.h.) were tallied on a strip 6.6 feet wide along the transect center line. Diameters were measured to the nearest 0.1 inch. Live seedlings were recorded on ten 2-milacre plots spaced at 1-chain intervals along the center line. Seedlings were classified as greater or less than 6 inches tall. Species were recorded separately except the seedlings of western and mountain hemlock, and western red- and Alaska cedar.

The study was expanded further to investigate the observed relationship between site quality and redcedar prevalence. A total of 142 yield plots previously taken in young, even-aged stands, within the range of redcedar, were examined to see if a relationship between site index and redcedar prevalence existed. Plots varied in size from

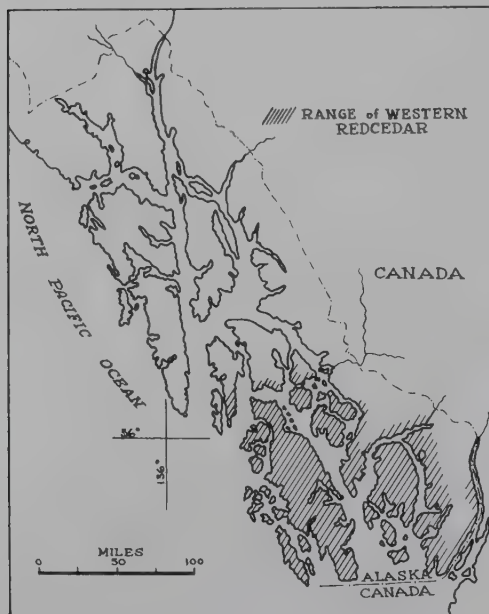


FIG. 1. Map showing range of western redcedar in Southeast Alaska.

1/27-acre in very young stands to 1 acre in older stands. Ages varied from 47 to 187 years.

Diameter distribution patterns were obtained for redcedar and western hemlock for each transect (Table I, Fig. 2). Mountain hemlock, Alaska cedar, and Sitka spruce were not included in the data analysis since they were very minor components of the stands.

TABLE I. Number of live seedling and sapling stems per acre for each area sampled and all areas combined

Area	Species	SEEDLINGS		SAPLINGS	
		Height - inches		D.b.h. - inches	
		< 6	> 6	1.0 - 2.9	3.0 - 4.9
1.....	WH	57,013	6,997	120	50
	WRC	23,848	71	..	..
2.....	WH	16,400	7,200	80	10
	WRC	10,750	..	..	..
3.....	WH	24,907	1,666	267	50
	WRC	7,164	..	17	..
4.....	WH	17,400	6,950	170	50
	WRC	12,300	100	10	10
5.....	WH	9,150	6,100	300	20
	WRC	11,950	300	..	..
6.....	WH	3,750	4,400	260	10
	WRC	5,150	..	10	..
Av., all areas	WH	21,437	5,552	200	32
	WRC	11,860	78	6	4

RESULTS

Occurrence of Redcedar in Old-growth Stands

Very marked differences in size class distribution were found to exist between cedar and hemlock. The average for all areas revealed that 21 percent of hemlock seedlings are in the "greater than 6-inch" class. Only 0.7 percent of the cedar seedlings, however, were 6 inches or taller. Very

few redcedar saplings and poles were encountered yet hemlock was quite abundant in these stages. The diameter distribution of redcedar (Fig. 2), though erratic, suggests an even-aged stand because of the comparatively few stems in the smaller diameter, and many stems in the mid-diameter classes. The number of hemlock stems rapidly decreases as d.b.h. increases, displaying a typical all-aged distribution. These data indicate that redcedar does not reproduce itself to an appreciable extent in well-stocked, old-growth stands. Schmidt (1955), observing a situation similar to this in the coastal forests of British Columbia, attributed the scarcity of advanced regeneration to probable germination failure and seedling mortality. Germination failure does not appear to be an important factor in Southeast Alaska, however, as an abundance of cedar seedlings were found on all areas. Some factor or combination of factors other than germination failure limits redcedar beyond the early seedling stage.

Either insufficient light or low temperatures appear likely as factors limiting redcedar seedling survival since this species will survive in the open. Schmidt (1955) observed that redcedar reproduced itself in open-grown stands on sites of exceptionally low productivity. Andersen (1953) suggests that temperatures during the growing season may largely determine the limits of the range of redcedar in Alaska which indicates that minor changes in temperature near the edge of its range may strongly affect its behavior. Baker (1934), in discussing tolerance, states: "The warmer the climate, the more tolerant a tree becomes. A tree which is tolerant in its optimum range may become half tolerant in a cooler re-

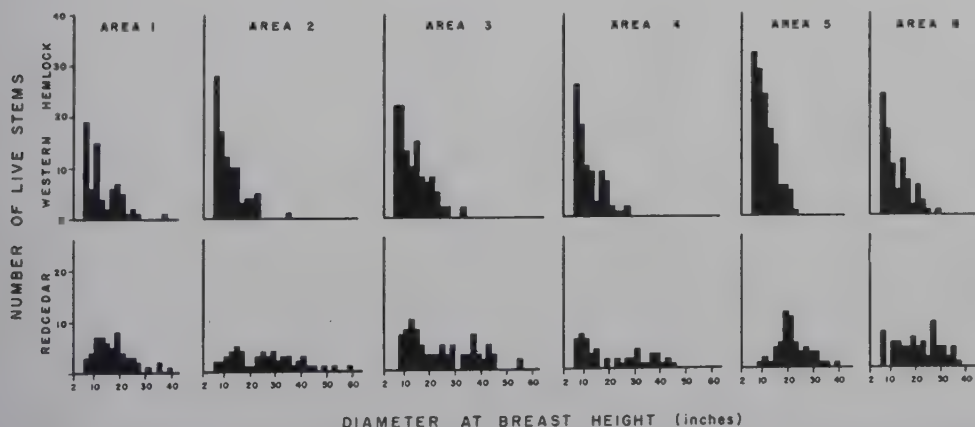


FIG. 2. Diameter distribution in old-growth cedar-hemlock stands by 2-inch d.b.h. classes for live stems 5.0 inches and larger. Per acre basis.

gion." Sudworth (1908) rated redcedar as most tolerant toward its south and lower limits.

Relationship between site index¹ and prevalence of redcedar

A definite relationship exists between site index and prevalence of redcedar (Table II). Some cedar was nearly always encountered in stands of site index 110 and less. Above site index 110 the frequency of cedar was much reduced. Practically no cedar was found in stands of site index 130 and higher.

TABLE II. Relationship between site index and occurrence of redcedar in young, even-aged stands.¹

Site index	No. plots	% of plots with redcedar	% OF STAND BASAL AREA IN REDCEDAR	
			Average	Standard dev.
66-75	3	100	57	...
76-85	16	94	22	± 14
86-95	15	100	20	± 15
96-105	20	97	17	± 14
106-115	18	89	12	± 12
116-125	38	34	1	± 4
126-135	19	1	< 1	± 2
136-145	3	...	...	...
146+	1	...	...	...

¹Based on stems 1.0 inches d.b.h. and larger

Percent redcedar by basal area was found to be highest in low site index stands, and lowest in high site index stands. Considerable variation existed between plots within each site index class, however, as shown by the large standard deviations (Table II). Factors other than site quality must affect species composition to an appreciable extent. The species composition of the seed source, prevalence of tolerant advanced regeneration, and seedbed conditions are variable factors known to influence stand composition.

Many of the lower site index plots had a fire history. Of the 26 areas in which young-growth plots were located, 8 showed evidence of an earlier burn. Average site index of plots on these burned areas was 96. This suggests that fire may have caused site deterioration. Occasionally, temporary reduction of site productivity may have occurred due to destruction of organic layers on shallow, rocky soils. On many of the plots having a fire history, however, fire-killed cedar snags were often quite abundant showing that the site was, most likely, within the lower productivity range before the fire. The association between fire history and prevalence of cedar is probably due to the high flammability of this species.

¹ Average height of dominant and codominant trees of spruce and hemlock at 100 years of age.

Species composition in terms of basal area seems to remain constant over a period of time in young, even-aged stands. Twenty-five plots which were established in 1927-30 were remeasured in 1948. Species composition remained almost the same (Table III). An additional analysis by site index classes showed no appreciable differences in species composition with time. Survival of redcedar is apparently effected during early stages of stand development. Once established in the stand cedar appears to hold its own, probably until the stand breaks down and cedar is replaced by hemlock in natural succession.

TABLE III. Difference in species composition over an 18 to 21 year period. Average of 25 plots

Date	% OF TOTAL STAND BASAL AREA		
	Hemlock	Spruce	Cedar
1927-30	52	36	12
1948	47	39	14

SUMMARY

Studies were made of the occurrence of western redcedar in old-growth uneven-aged and young even-aged stands in Southeast Alaska.

It was found that redcedar does not reproduce itself to an appreciable extent in well-stocked old-growth stands. Cedar seeds germinate and young seedlings are numerous but they fail to survive. It appears that the direct effect of light or its indirect effect through warming of the site is necessary for survival of this species in Alaska. Redcedar is at the northern limits of its range in Southeast Alaska and is probably very sensitive to slight environmental differences.

A definite relationship between site index and prevalence of redcedar was found. Some cedar was nearly always encountered in stands of site index 110 and less. The occurrence of cedar was much reduced above site index 110 and very seldom encountered in stands of site index 130 and higher. Percent redcedar by basal area was found to be highest in low site index and lowest in high site index stands.

Most of the lower site index areas on which young-growth redcedar was prevalent had a fire history. Examination of the trees killed by the fires showed that cedar was usually present in the old-growth stands before they were burned. The association between fire history and prevalence of cedar is probably due to the high flammability of this species.

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NOTES AND COMMENT

DENSITY OF WOOD RAT HOUSES IN ARIZONA CHAPARRAL

Data on the abundance of small mammals are not plentiful, and of 125 papers including such data that were reviewed by Mohr (1943, 1947) only three gave information on the density of wood rats.

The density of houses of white-throated wood rats (*Neotoma albigula*) on a tract of 8.5 square miles, located 10 miles west of Prescott, Arizona, was estimated. The tract was used principally as a study area for mule deer (*Odocoileus hemionus*) and has been described in detail elsewhere (Hanson and McCulloch 1955: 568-569). Average elevation is about 5,000 feet. The vegetation is chaparral, of which shrub live oak (*Quercus turbinella*), skunkbrush (*Rhus trilobata*), and mountain mahogany (*Cercocarpus montanus*) are the dominant plants. Some open, grass-covered areas were present, but nearly all of the study area was thought to be suitable habitat for wood rats.

On the study area, 30 transects, each 300 feet by 20 feet, were located at random. All transects occurred where there were numerous shrubs except one which was in a grassy opening. Although the transects were established in order to count deer pellet groups, wood rat houses also were counted when the pellet groups were removed, which was mainly during the first half of winter 1954-55.

Twenty-seven houses were found on the 4.132 acres included in the transects; 21 of these, or about 78 per cent, were in active use. The mean number of occupied houses per transect was 0.700, but the number of wood rats living in the houses was not learned. The sample did not differ significantly from the Poisson distribution according to the Chi-square test. The standard error of the mean was calculated as ± 0.15 and the fiducial limits, at the 0.95 level, were 0.31. The number of occupied

houses per acre averaged 5.1 but may thus have ranged from 7.3 to 2.8.

On a 750-acre tract in southeastern Arizona and southwestern New Mexico, 91.4 per cent of the houses were in active use, and 2.3 occupied houses of white-throated wood rats were present per acre (Monson and Kessler 1940: 42).

The bark of skunkbrush was extensively utilized on the Prescott study area. Prickly pear cactus (*Opuntia* spp.) and other cactuses were not common on most of the area, but evidently the wood rats were thriving with the bark of skunkbrush as a staple food. Wood rats helped to control the skunkbrush, which is not commonly eaten by deer or cattle and tends to increase at the expense of other plants.

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SOME ASPECTS OF MICROCLIMATE IN A PINE FOREST AND IN AN ADJACENT PRAIRIE¹

INTRODUCTION

An accurate method of assessing evaporation or water loss from the soil has not been demonstrated to date (Thornthwaite 1940). An experiment was designed to test the Lowry (1956) method of measuring water loss from the soil. The sites were located in a pine forest and in a prairie in the University of Wisconsin Arboretum. Variations in temperature and humidity were also recorded for the two sites over a period of 17 days. The two sites were situated on the same soil type, "Miami silt loam." The 23-year-old forest called the "Leopold Pines" consisted of red pine (*Pinus resinosa* Ait.) which had been planted with random spacing at a density of 1,700 trees per acre. They had reached an average height of approximately 45 ft. by 1955. The planted prairie, adjacent to the forest, consisted mainly of the bluestems (*Andropogon scoparius* Michx., *A. gerardi* Vitman.) and Indian grass (*Sorghastrum nutans* (L.) Nash.). The straw-colored culms of the previous season's growth averaged 2.5 ft. in height. Spring growth was barely

evident in the open and entirely absent in the forest when the experiment was initiated.

The authors are indebted to Dr. R. A. Bryson of the Department of Meteorology and to Dr. J. T. Curtis of the Department of Botany at the University of Wisconsin for suggestions and constructive criticism.

METHODS

The Lowry (1956) evaporation method was used; evaporation was measured from soil in a water-tight metal pan 10 cm. deep and having 1000 sq. cm. cross sectional area. In the present experiment, two aluminum pans 30 cm. x 30 cm. x 8.75 cm. were used at each site, one being water tight and the other permitting water to percolate through the bottom of the pan. The holes were made with a 9-gauge nail at 1 in. intervals. The procedure of installation of an evaporation pan involved removing a block of soil with as little disturbance as possible and inserting it into the pan. The pan was then fitted into the hole and the surface debris replaced. A hygrothermograph was placed at each site under a shelter constructed of plywood (painted white for maximum light reflection). The hygrothermographs were calibrated

¹Contribution from the University of Wisconsin Arboretum, Journal Paper No. 36.

for humidity with a dewcel (Conover 1950). The evaporation pans were weighed daily (within 0.1 per cent) at various intervals throughout a 24-hour period for 17 days commencing April 25, 1955 to determine water loss in gm. per 900 sq. cm. of surface area. An attempt was made to correlate the amount of water loss from the pans in a given time with the area (measured by a planimeter) circumscribed above the relative humidity curve but below the 100 per cent humidity line on the chart of the hygro-thermograph. The area above the relative humidity curve (which decreases as the humidity increases) is presumed to approximate the vapor pressure deficit. This assumption is valid only when temperature is constant. By measuring temperature in degrees Absolute however, the variation is relatively small (Lowry 1956).

RESULTS

Evaporation

The loss of water in gm. per 900 sq. cm. of soil surface from both pans located in the prairie (when plotted on log-log paper against the values obtained from planimetered areas) approximated a slope = 1 as determined by linear regression (Snedecor 1946). The regression line for the pan without holes is shown in Figure 1.

Prairie site-pan without holes

x-day reading

•-night reading

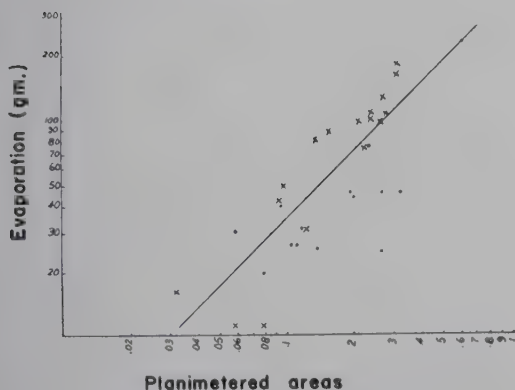


FIG. 1. Water loss in gm. plotted against planimetered areas representing vapor pressure deficit.

Lowry (1956) obtained similar results from an evaporation pan with a water-tight bottom located in a semi-open pine-fir forest in California. Using the corner test of association (Olmstead and Tukey 1947) in the present experiment, the peripheral points were significant to the 0.1 per cent level for the pan without holes (Fig. 2) and beyond the 0.1 per cent level for the pan which permitted water drainage (Fig. 3). Dots represent day readings in both figures. The dots and crosses are somewhat segregated, indicating greater water loss during the day. Water loss from the pan with holes exceeded that from the pan without holes by 12.8 per cent. Evaporation was consistently higher from the pan without holes, being particularly evident for a period of two days following each rain.

Prairie site-pan without holes

Quadrant sum

$s = 21$

$p = 0.1\%$

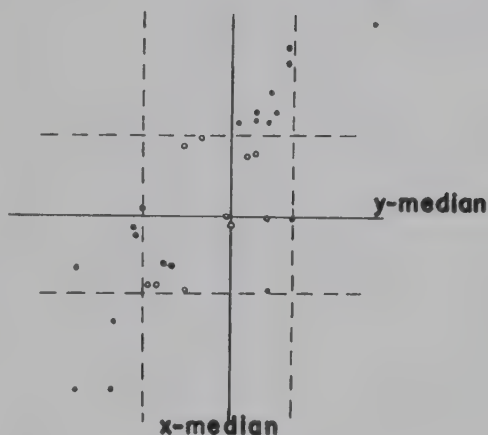


FIG. 2. A corner test for association on a scatter diagram representing 31 pairs of observations. Top = +9, right = +1, bottom = +4, left = +7.

Prairie site-pan with holes

Quadrant sum

$s = 30$

$p < 0.1\%$

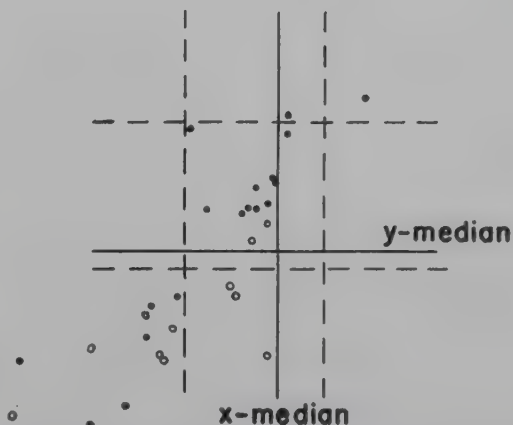


FIG. 3. Corner test for association on a scatter diagram representing 29 pairs of observations. Top = +2, right = +1, bottom = +15, left = +12.

The water loss in the open was 410.6 per cent greater than in the forest (Table I). Water loss in the forest was often little more than 0.1 per cent of the soil weight in the pan except when the soil moisture was above field capacity. The scattering of the points when plotted on log-log paper illustrates no definite trend of water loss from either pan. The corner test for association (Olmstead and Tukey 1947) did not reveal a significant association of the peripheral points (Fig. 4). Identical values for P were obtained for evaporation from the two pans in the forest.

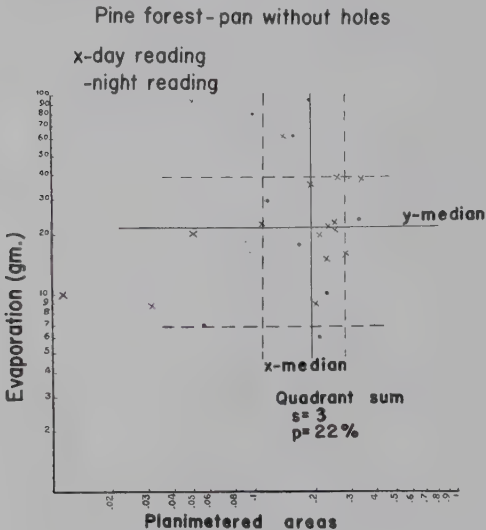


FIG. 4. A corner test for association on a scatter diagram representing 25 pairs of observations. Top = -5, right = +2, bottom = -1, left = +1.

TABLE I. The mean and range of maximum and minimum temperatures (°F.) and relative humidity, and mean water loss in gm. per 900 sq. cm. of soil surface area for a 24-hour period in forest and open. The mean delay in time of occurrence in forest compared with the open is given for temperature and humidity maxima and minima.

	Open	Forest	Delay in hrs. of occurrence in forest
Max. temp. range...	52- 93	47-81	
Mean max. temp....	79.1	67.3	+1.8
Min. temp. range...	36- 58	43-60	
Mean min. temp....	46.6	50.3	+1.5
Max. humidity range	70-100	65-95	
Mean max. humidity	94.5	89.0	+1.8
Min. humidity range	8- 44	14-61	
Mean min. humidity	23.1	30.6	-0.5
Mean water loss (gm.)	134.8	26.4	

Temperature

Temperature data are summarized in Table I. During the period April 25 to May 12, 1955, the temperature 20 cm. above the ground varied between 36° F. and 93° F. in the open; between 43° F. and 81° F. in the forest. The mean temperature however in the open (62.0° F.) was 4°

higher than the mean temperature in the forest. The daily maximum temperature in the open ranged from 2° to 21° higher than in the forest with a mean of 11.0° F. The daily maximum temperature was reached at approximately 2 p.m. in the open (except when rain occurred) and an average of 108 minutes later in the forest. The mean minimum temperature in the forest (50.3° F.) occurred 90 minutes later than the mean minimum temperature (46.6° F.) in the open (Table I). Each recording of time was determined to the nearest 15 minutes.

Relative Humidity

The extreme high and low humidity readings in the forest were moderate compared with those in the open. Relative humidity varied from a high of 100 per cent to a low of 8 per cent in the prairie, compared with a high and low of 95 per cent and 14 per cent respectively, in the forest. The mean humidity was between 58 and 60 per cent in both forest and open. The mean daily maximum humidity in the forest was 94.5 per cent, compared with 89.0 per cent in the prairie. The mean daily minimum humidity in the grassland was 23.1 per cent, compared with 30.6 per cent in the forest (Table I).

DISCUSSION

The pan with holes provides a more realistic measure of water loss than the pan without holes, since it permits water in excess of field capacity to drain through the pan into the soil. This would appear to have some merit since the evaporation data from the pan with holes revealed a higher degree of association with vapor pressure deficit. Since the data provide a straight line with a slope of approximately 1, it appears possible that the relative humidity recorded by a hygrothermograph may indicate approximate water loss from the soil in the prairie. This method has been suggested as practical for measuring evaporation in the forest (Lowry 1956). The area could be "calibrated" by weighing the evaporation pan 3 to 5 days after it was set out. This period of time would be sufficient to cancel out the diurnal effects which are evident when measurements of water loss are taken at shorter intervals. The limitations of the method according to Lowry are based on assumptions of uniform wind, air temperature and surface soil moisture throughout the estimation period. Diurnal temperature effects may be cancelled out as suggested above. Any rainfall occurring during the estimation period would necessitate a recalibration of the area. During the present experiment, rainfall which occurred on three occasions had little effect due to the fact that weighing the evaporation pans at short intervals permitted detection of the increase in moisture expressed as an increase in weight.

The lack of a definite trend of water loss and lack of significant association of the peripheral points from forest evaporation pan data would indicate that the method is not applicable for measuring soil water loss in a dense red pine forest in Wisconsin. A possible explanation may be that evaporation in the forest is of inadequate quantity to express a significant association. Applying this line of reasoning to evaporation in the open, the corner test for association was applied to evaporation values of the same magnitude that were found in the forest. The peripheral values were significant at the one per cent level for the pan without holes, and beyond the 0.1 per cent level for the pan with holes. The evidence from these data would suggest that in the open, vapor pressure deficit has a strong influence on water loss from the soil. In the forest however, it would appear that the

effect of vapor pressure deficit is masked by the influence of other micro-environmental factors.

Bates (as quoted by Geiger 1950) reported the diurnal temperature range to be more extreme in windbreak strips than in the open. The same may apply within a forest plantation (Niederhoff and Stahelin 1940). Diurnal temperature variation increases with the size of the opening in a forest (Geiger 1950) by permitting increased day insolation and increased night radiation. The tree canopy retards mixing of the air, resulting in severe diurnal temperature variation. Aikman (1938), however, found that the "lows" and "highs" of temperature were less variable in the forest than in the prairie. Results similar to Aikman's were obtained in the "Leopold Pine Plantation." The fact that the temperature regime was similar to that of a forest as opposed to that of a plantation may indicate that the irregular spatial pattern of the trees in a forest is a significant factor in the modification of temperature. This factor alone could conceivably contribute to more vigorous forest growth.

Maximum relative humidity occurred shortly after sunrise in the prairie and with the exception of rainy periods was coincident with low temperature. The high humidity in the forest occurred approximately two hours later and was generally coincident with low temperature. Similarly in the open, low relative humidity and high temperature occurred almost simultaneously. The humidity minimum in the forest preceded the humidity minimum in the prairie by a mean of one-half hour. Consequently during 24 hours the high humidity period was sustained 2.5 hours longer in the red pine forest than in the open. This tendency is accentuated under tropical conditions where the period of high humidity in the rain forest is 7 hours longer than it is in an adjacent grassed area (Hales 1949).

A close examination of hygrothermograph traces in forest and open indicate differences in the character of these traces. The trace approaching low humidity in the open is a relatively smooth line with almost imperceptible oscillation. The low humidity trace in the forest demonstrates a general trend with numerous minute oscillations. This may indicate a relatively greater influence by the forest micro-environment. The trace of increasing temperature displayed a sharp peak in the open prior to the initiation of a decrease. The peaks of temperature in the forest were flat-topped, demonstrating the conservative influence of forest vegetation. These temperature maxima were maintained from one to three hours.

The influence of the forest canopy in the modification of low humidity, the sustained period of high humidity, and the modification of high temperature are important factors operating for greatly reduced soil-water loss in a pine forest compared with an adjacent prairie environment.

SUMMARY

Some aspects of microclimate were measured in a planted red pine forest, and in a prairie at the University of Wisconsin Arboretum. Water loss from the soil was measured by the Lowry (1956) method. Water loss from soil in pans (30 x 30 x 8.75 cm.) at the ground surface

indicated relative humidity to be an approximate measure of evaporation in the open. A line with a slope =1 was approximated by plotting on log-log paper the area representing the vapor pressure deficit on the chart of a hygrothermograph against gm. of water lost per unit time. The corner test of association showed the association of peripheral points to be significant at the 0.1 per cent level. Pans which permitted water drainage lost 12.8 per cent less water through evaporation than pans without holes and provided data with a higher degree of statistical significance. Water loss in the open exceeded that in the forest by more than four times. The scattered points representing water loss in the forest revealed no definite relationship between evaporation and relative humidity, and the peripheral points were not significantly associated.

The forest canopy modified the extremes of temperature and humidity and maintained longer periods of higher humidity than the grassland. Random distribution of the trees in a forest or plantation may be an important factor in the modification of temperature extremes as compared with a plantation of regularly spaced trees.

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VASCULAR EPIPHYTES IN THE GREAT SMOKY MOUNTAINS¹

Vascular epiphytes such as orchids and bromeliads are a conspicuous part of the moist forests of the tropics and subtropics. In temperate eastern North America, however, they are rare and nearly all the epiphytes are lichens, mosses, or hepatics.

One common exception is *Polypodium polypodioides*



FIG. 1. *Betula alleghaniensis* in the Smokies with large horizontal branch supporting several epiphytic *Picea rubens* saplings one of which has a diameter of 3 inches. Note fog in background. Photo by courtesy of Jim Thompson.



FIG. 2. Two young epiphytic *Picea rubens*, the larger about 20 inches tall, which started in a knothole in a branch of *Betula alleghaniensis*. Note abundance of non-vascular epiphytes, mainly lichens.

¹ Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. No. 181.



FIG. 3. Epiphytic *Rhododendron maximum* growing below a crotch of *Betula alleghaniensis*.

(L.) Watt,² a fern often epiphytic in the part of the United States south from Iowa and Delaware.³ Polypody ferns have been studied and discussed in some detail by Johnson (1921) and Pessin (1925). The resurrection fern grows on trees in the lower elevations of the Great Smoky Mountains. However, less well known are the occurrences of Spermatophytes as epiphytes on trees, particularly *Betula alleghaniensis* Britt., above 3,500 feet in the Smokies. I have counted the epiphytic seed plants between Alum Cave Parking Lot (3,850 feet) and Walker Prong (4,500 feet) along the trans-mountain highway that leads from Gatlinburg, Tennessee, to Newfound Gap. In a distance of about four miles I saw 17 *Rhododendron maximum* L., 6 *Picea rubens* Sarg., 2 *Tsuga canadensis* (L.) Carr. and 1 *Diervilla sessilifolia* Buckl., all epiphytic on yellow birch, *Betula alleghaniensis*. On the steep north slopes of Mt. LeConte, I have seen the following as epiphytes: *Acer rubrum* L., *Ribes cynosbati* L., and *Rubus canadensis* L. on yellow birch; and *Clethra*

² Now designated as var. *michauxianum* Weath., and often referred to as the resurrection fern.

³ The epiphytic Spanish moss, *Tillandsia usneoides* L., with a more southern distribution has been studied by Billings (1904) and Penfound and Deiler (1947).

acuminata Michx. on chestnut oak, *Quercus prinus* L. (*Q. montana* Willd.).

Not all of these vascular epiphytes are young seedlings. Some have matured enough to reproduce; I have seen mature cones on *Picea rubens* and flowers and fruits on both *Rhododendron maximum* and *Diervilla sessilifolia*. Moreover, the epiphytes may grow until rather large (Fig. 1).

Another vascular epiphyte which is common (perhaps most common) in the Smokies is *Betula alleghaniensis*. Because it as an epiphyte nearly always grows on another older *B. alleghaniensis*, it is difficult to distinguish between branches resulting from adventitious buds as figured by Cain (1940) and true epiphytic plants. Cain (l. c.) described and illustrated individuals of *B. alleghaniensis* which originated on logs and stumps and later became "trees on stilts" with aerial roots.

The epiphytic vascular plants often begin life, sometimes 40 to 50 feet above the ground, in knotholes (Fig. 2), near crotches (Fig. 3), in crevices of bark and even in the moss on the upper surfaces of large branches (Fig. 1). The germination of seeds in such positions and the subsequent growth of the epiphytes are permitted by the high precipitation and high humidity of the Smokies, particularly above 3,500 feet where the slopes and valleys are often bathed in fog. That there can be considerable surplus of precipitation over evapotranspiration in the Smokies has been indicated by Shanks (1954).

Shanks (l. c.) concluded that the Smoky Mountain climates above 2,500 feet fall into the *rain forest class*. This conclusion is reinforced by the presence of vascular epiphytes as well as large numbers of non-vascular epiphytes which are so characteristic of rain forests.

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A STUDY OF THE LOBING OF SUN AND SHADE LEAVES¹

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INTRODUCTION

This study aims to determine whether leaves which have a tendency to lobe will be more lobate on the south periphery of a plant in direct sunlight than on the shaded side of the same plant. The study also considers briefly the external features of sun and shade leaves.

Chrysler (1904) found that leaves of maritime plants from the Atlantic coast were from once to more than twice as thick as leaves of inland plants from the vicinity of Chicago, Illinois. He considered the increase in thickness due principally to the development of palisade cells. He believed the greater compactness of the tissue of the leaves from the Atlantic coast was probably caused by the amount of salt.

Copeland (1904) discovered great variations in the shape and thickness of the leaves from the same branch. Bergen (1909) ascertained that the upper surfaces of leaves freely exposed to the sun were often concave and such that the concavity lessened or disappeared in shade leaves. Hanson (1917) showed that leaves from the south periphery of a tree were more deeply lobed, more prominently toothed, and smaller than leaves from the center of the same tree.

Coulter, Barnes, and Cowles (1931) found that in *Geum virginianum* L. and *Ranunculus abortivus* L. the basal rosettes of roundish leaves were succeeded upward by

variously divided stem leaves. In *Silphium laciniatum* L. the early leaves were narrow and undivided and were succeeded upward by broader, lobed leaves. In various oaks the early leaves were entire and the adult leaves were lobed. The lobation of the upper leaves, as well as the smaller size and greater thickness, was thought to result from a low water supply.

Coulter, Barnes, and Cowles (1931) recorded that in species of *Morus*, the more lobate leaves were usually smaller and on slender branches, while the simple leaves were on luxuriant shoots. *Lactuca* and *Lepidium* showed thin, entire shade leaves, and thick, lobed sun leaves. *Leonurus cardiaca* L. leaves were more divided in the intermediate stem region than the leaves above and below the middle of the stem. In *Cytisus scoparius* L. the three-lobed lower leaves were succeeded by one-lobed leaves. In *Sassafras sassafras* (L.) Karst. the leaves were entire or lobed regardless of the environmental factors affecting leaf variation.

These authors stated also (1931) that still another variation occurred in certain plants whose asymmetrical leaves were thought to be caused by unequal illumination. The chief determining factors of leaf size and proportion were those that control water supply. High transpiration, whether caused by dry soil, salts, low oxygen pressure, or low temperature, was probably the dominating influence in determining the small size and the great thickness of xeric leaves.

Weaver and Clements (1938) concluded that the outlines of shade leaves were more nearly entire than those of similar leaves grown under strong insolation. A correlation appeared between lobing of leaves and rate of water supply and water loss from the plant, but more experimental work was needed to establish this relationship.

METHODS

Leaves from plants showing a tendency to lobe were collected from ten species of herbs, ten species of shrubs, and seventeen species of trees in the Denver and surrounding plains area, and the nearby foothills of the Rocky Mountains. The sun and shade leaves were taken from the south and north peripheries, respectively, of the same tree or shrub. Leaves from the herbs were collected from several plants. A minimum of twelve sun leaves and twelve shade leaves of each species was selected. Care was taken to secure leaves from the middle of a branch or stem rather than from the base or tip in order to maintain comparative results when considering the average lobed leaf. (Fig. 1). The sun and shade leaves were collected from the same height on each plant of the species.

The external features of coloration and texture of the leaves were carefully studied. The average thickness of the sun and shade leaves was measured to the thousandth of an inch with a micrometer. Blueprints were made of one shade leaf and one sun leaf from each of the plants studied. These leaves were of an average type, being neither as lobed as some sun leaves nor as entire as some shade leaves. A planimeter was used on the blueprints to measure the square inches of leaf area. The perimeters were measured with a Universal Map Measurer in linear inches. The petioles were measured from the actual leaves.

A mathematical proportion between the leaf perimeters and leaf areas was used to determine the percentage that the proportional perimeter was of the actual perimeter and the lobing of the shade leaves was compared with that of the sun leaves. The proportional perimeter is that perimeter which should replace X to keep the perimeters and areas in the same proportion. For example:

$$\begin{array}{l} \text{Shade leaf} \qquad \qquad \text{Sun leaf} \\ \text{Perimeter : Area :: Perimeter : Area} \\ 12.5 : 7.6 :: X : 6.30 \\ 7.6X = 12.5 \times 6.30 = 78.750 \\ X 78.750 = 10.36, \text{ the proportional perimeter.} \\ 7.6 \end{array}$$

Where 19 is the actual perimeter, $\frac{10.36}{19} \times 100\% = 54.5\%$.

RESULTS

The results of the study are presented in extensive tables in the thesis library of the University of Denver. Some of the most outstanding leaf variations are pictured in Figures 2, 3, and 4. We particularly wish to point out the great difference between the sun and shade leaves of *Morus pendula* L. and those of *Lactuca canadensis* L., found in Figures 2 and 4, respectively.

The individual points of interest relative to the study of the exterior of the sun and shade leaves are too numerous to mention in this article. However, it should be stated that the majority of the sun leaves were darker in color and hairier of surface than the shade leaves. The veining and marginal serrations were more pronounced in the sun leaves than in the shade leaves.

The percentages given below briefly summarize the results of the study.

1. Ninety-one and eight-tenths per cent of the sun leaves were more deeply lobed than the shade leaves.
2. Fifty-seven per cent of the perimeters of the shade leaves were larger than those of the sun leaves.
3. Seventy-eight per cent of the shade leaves had larger areas than the sun leaves.

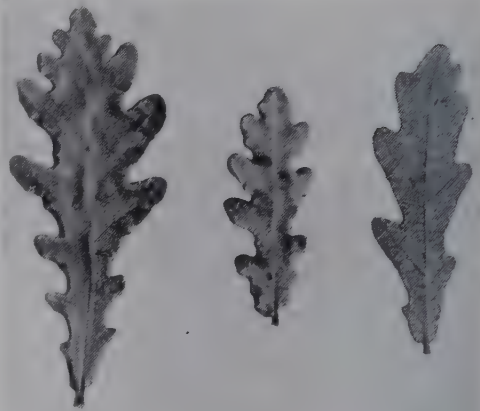


FIG. 1. *Quercus gunnisonii* leaves, showing left to right, leaf from tip of branch, sun and shade leaves from middle of branch.

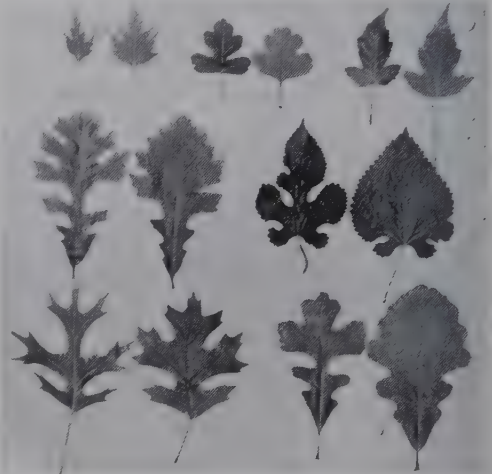


FIG. 2. Tree leaves. Row 1, left to right (as in all of the remaining figures), sun and shade leaves of *Betula laciniata*, *Crataegus marshalii*, and *Acer rubrum*. Row 2, *Quercus stellata* and *Morus pendula*. Row 3, *Quercus velutina* and *Q. macrocarpa*.

4. Sixty-five and nine-tenths per cent of the petioles of the shade leaves were longer than those of the sun leaves.

5. One hundred per cent of the sun leaves were thicker than the shade leaves.

DISCUSSION

Of the thirty-seven species studied, the areas of twenty-nine of the shade leaves were larger than those of the sun leaves. The perimeters of the shade leaves of twenty-one species were greater than those of the sun leaves. Since the lobes of the shade leaves do not have as deep indentations as those of the sun leaves, the perimeters of the sun leaves would be greater than those of the shade



FIG. 3. Shrub leaves. Row 1, *Ribes parvulum* and *Rhus trilobata*. Row 2, *Quercus gambelii* and *Viburnum trilobum*. Row 3, *Bossekia deliciosa* and *Viburnum opulus sterilis*.



FIG. 4. Herb leaves. Row 1, *Chrysanthemum morifolium* and *C. morifolium* (yellow flowered). Row 2, *Chrysanthemum coronarium* and *Ambrosia artemisiifolia*. Row 3, *Lactuca canadensis*, sun leaf, shade leaf, and swamp leaf grown in full sunlight.

leaves even if the leaf areas of the sun and shade leaves were the same.

Many causes have been assigned to explain the differences in the ratios of areas to perimeters of sun and

shade leaves. One of the more important factors is the cellular structure of the leaves previously mentioned in the introduction. The sun leaves have better developed palisade tissue than the shade leaves, while the latter have more parenchyma tissue. The presence of more parenchyma in the shade leaves, consisting of large spongy cells with many intercellular spaces, could conceivably increase the area of the leaf. Thus the lobation would be comparatively less acute. The more highly developed palisade tissue in the sun leaves, consisting of elongated cells, would tend to thicken the leaf, and thus produce a more compact leaf structure with possible increases in the depth of the lobes.

It would appear that environmental factors are of importance in the production of leaf variation. Climatic zones seem to influence the amount of lobation occurring within the same species of plant. Water supply also seems to affect leaf variation. *Lactuca canadensis* L. leaves collected from a swampy area but receiving full sunlight were much larger than the sun leaves gathered from a dry garden plot (Fig. 4).

The rate of transpiration from the sun leaves tends to shrink the leaves by removing water from the cells of the mesophyll and consequently to produce a greater amount of lobing. Since there is not so much water loss in the shade leaves, the areas of the latter are larger than those of the sun leaves and the lobing is decreased.

Plant branching and leaf shape are also contributing factors to leaf variation. For example, the leaves of *Acer saccharinum* L. are lace like and allow the sun to filter through the leaves and branches. Therefore, there is less leaf variation between the leaves of the south and north exposures of such a plant.

SUMMARY

1. Leaves were collected from the south and north peripheries of ten herbs, ten shrubs, and seventeen trees. The shade leaves were procured from the same height as that of the sun leaves. The leaves were taken from the middle of the branch rather than from the base or tip. The leaves were pressed dry after picking from the plants.

2. Blueprints were made of one sun leaf and one shade leaf from each plant. From the blueprints the areas of the leaves were measured in square inches with a planimeter. The perimeters were measured in linear inches with a Universal Map Measurer. A micrometer was used to determine the thickness of the leaves. The petioles were measured to the thirty-secondth of an inch from the actual leaves.

3. A simple proportion between the perimeters and areas of a given species was used to determine the percentage that the proportional perimeter was of the actual perimeter. From these results, the percentage of the lobing of the shade leaf to the sun leaf was calculated.

4. Fifty-seven per cent of the perimeters of the shade leaves were larger than those of the sun leaves.

5. Ninety-eight and eight-tenths per cent of the sun leaves were more deeply lobed than the shade leaves.

6. A study of the exterior of the sun and shade leaves showed the majority of the sun leaves to be darker in color and with more hairy surfaces than the shade leaves. The veining and marginal serrations were more pronounced in the sun leaves than in the shade leaves.

7. The petioles of the shade leaves were sixty-five and nine-tenths per cent longer than those of the sun leaves.

8. The sun leaves were one hundred per cent thicker than the shade leaves.

9. Seventy-eight per cent of the shade leaves had larger areas than the sun leaves.

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SIR ARTHUR TANSLEY AND THE SCIENCE OF ECOLOGY

Sir Arthur Tansley, eminent British ecologist, pioneer in that youthful science, active in other fields as well, died on November 25, 1955, at the age of eighty-four. A Resolution of Respect, in which an outline of his life and accomplishments was included, appeared in the *Bulletin of the Ecological Society* shortly after his death.¹

It seems appropriate that a fuller account of certain aspects of his career—the role he played as a pioneer in the science of ecology and his influence in its continued development—should be made available to ecologists in America, where his contributions, unspectacular perhaps, but pervasive in their influence, may not have received their full meed of appreciation. This essay is offered as a tribute of admiration and friendship for A. G., as Sir Arthur liked to be called by his friends.

In the late nineties appeared two epoch-making works that became foundation stones for the science of ecology: Warming's *PLANTESAMFUND* and Schimper's *PFLANZEN-GEOGRAPHIE AUF PHYSIOLOGISCHER GRUNDLAGE*. The impact of these was felt in Britain and America at about the same time. The German translation of Warming's work was widely read in England and doubtless influenced the thinking of many botanists. Inspired by Warming and Schimper, Cowles in 1899 and 1901 and Clements in 1904 produced their classic works.

Tansley (1947) has told us of the beginnings of plant ecology in Britain: "I well remember working through [Warming's book] with enthusiasm in 1898 and going out into the field to see how far one could match the plant communities Warming had described for Denmark in the English countryside; and I also made the book the basis for a course of University Extension lectures at Toynbee Hall in 1899." The German edition of Schimper of course added its influence, as did Flahault's work at Montpellier.

Tansley characteristically gives ample credit to a number of British botanists who at this time were conducting local vegetation surveys. Nevertheless it was Tansley who, in a paper read before the British Association in 1904, suggested the formation of a central committee for the systematic survey and mapping of the vegetation of the British Isles. In December of that year four men—Tansley, C. E. Moss, W. G. Smith, T. W. Woodhead—met to make plans for the establishment of such a group. It was resolved to form the "Central Committee for the Survey and Study of British Vegetation"; Tansley became its leader and spokesman.

In 1908 Tansley joined a plant-geography tour in Switzerland organized by Dr. Carl Schröter in connection with the International Congress of Geography at Geneva. Much impressed by the benefits it brought through acquaintance with diverse vegetation types and contacts made with botanists of other countries, he suggested to the Committee on his return that a similar international excursion be organized in the British Isles. The proposal met with immediate approval, and after preliminary correspondence invitations were sent to about a dozen foreign phytogeographers for a tour of the British Isles in August, 1911.

So came into being the first International Phytogeographic Excursion. The foreign scientists who participated were Rübel and Schröter (Switzerland), Drude and Graebner (Germany), Lindman (Sweden), Massart (Belgium), Ostenfeld (Denmark), and Clements and Cowles (United States).

The close tie that has existed between British and American ecologists in viewpoint and in method had its origin in this meeting, largely because Tansley, in this his first contact with Cowles and Clements, men so dissimilar in personality though fundamentally similar in their aims, understood and appreciated both.

In his account of the first I P E Cowles (1912) remarked: "It was the universal testimony that these international excursions must thenceforth be a feature of phytogeography." The feeling thus expressed found speedy realization; in Tansley's words, the event "inspired our foreign guests to go and do likewise." Thanks to the energy of Henry C. Cowles, with the assistance of George D. Fuller and George E. Nichols, a second I P E came into being in 1913. It covered the United States from coast to coast, and was a big and complicated operation, successful from beginning to end. Several of those who had participated in the first excursion were present, including Mr. and Mrs. Tansley, Schröter, and Rübel; in addition, from Europe, Dr. and Frau Brockmann-Jerosch, Skottsborg, Szafer, Stomps, Paulsen, and Herr Geheimrat Adolf Engler.

A third I P E, planned for Switzerland in 1915, abandoned on account of World War I, was carried through in 1923. In the inter-war period six international field gatherings were held. In addition to Switzerland, the regions visited were Scandinavia, Czechoslovakia and Poland, Rumania, Italy, and Morocco and Algeria. The influence of these events has been profound. Their success was due to cooperation among scientists of many nations; the Geobotanische Forschungsinstitut Rübel in

¹ Bull. Ecological Soc. Am. 37: 52. 1956.

Zürich must be given special mention. The initial impulse, however, was provided by Tansley; without him the idea would probably not have been born.

By 1912 it had become apparent that the small, informal British Vegetation Committee had accomplished its purpose and that, in view of the greatly increased number of workers on ecological projects, the time was ripe for the formation of a society which, since zoologists as well as botanists were beginning to recognize the ecological approach, should cover the animal as well as the plant field. On April 12, 1913, the British Ecological Society was formally constituted, and Tansley became the first president of the first society of ecologists the world had seen.

Simultaneously the *Journal of Ecology* began publication. In 1917 Tansley became its editor, a post which he held for 21 years. He had already, in 1902, founded the *New Phytologist* (now in its 56th year); he was its editor during its first 30 years. He contributed many reviews of current literature to the two periodicals; in the *Journal* alone, in the 21 years of his editorship, there are 67 initialed by him, some of them lengthy and detailed.

Tansley was always deeply interested in the teaching of botany, and ecology in particular. In the early days of the latter science he realized the impossibility of effective teaching in the classroom. He and C. E. Moss, at Cambridge, tried out one-half day and then full-day field trips, and later made excursions lasting several days. In 1914 he led an advanced class on an excursion to Provence and the Maritime Alps. In 1922 he published a small text book, *ELEMENTS OF PLANT BIOLOGY*, and later two guides to ecological research: *PRACTICAL PLANT ECOLOGY* (Tansley 1923) for beginners and, with T. F. Chipp, *AIMS AND METHODS IN THE STUDY OF VEGETATION* (Tansley and Chipp 1926) for advanced students.

Tansley's active mind refused to be confined within the bounds of a single science. He became absorbed in Freudian psychology and in 1920 published a book upon it: *THE NEW PSYCHOLOGY* (2nd ed. Tansley 1924). An excerpt from a letter received from him in November, 1923, while he was working with Freud in Vienna, reveals his state of mind at that period:

"In 1920 I published *THE NEW PSYCHOLOGY*, which, by the way, is *not* a text book, but intended for the general reader who wants to know something about the modern view of the mind. It has been very successful, over 10,000 copies selling in 3 years, about 4,000 in America. I am doing psychological work here now, having resigned my lectureship at Cambridge. . . . I shall continue to edit the journals and also to work at ecology, but I do not know to what this splitting of interest will eventually lead." When I talked with him a year later the uncertainty was still there. His subsequent activities prove that ecology won out. Psychology lost a clear thinker; ecology retained one.

A detailed analysis of Tansley's scientific writings will not be attempted here. It is sufficient to note that he carried out a considerable number of projects in field research and published upon them, alone and in collaboration with others. His greatest influence, however, lay in synthesis of individual studies done by several or many. The most comprehensive work of this kind is *THE BRITISH ISLANDS AND THEIR VEGETATION* (Tansley 1939). In recognition of this achievement he received

the Gold Medal of the Linnean Society of London. General concepts interested him far more than detailed studies; the concept of the ecosystem is a case in point. His thoughts were always clothed in language of admirable clearness and precision.

In the post-World War II period of reconstruction, nature conservation became his prime interest. Already, in 1942, he had become chairman of a committee of the British Ecological Society, charged with formulation of a policy with regard to nature reserves. This led to establishment in 1949 of the Nature Conservancy, a department of government, of which Tansley became the first chairman. His services in the field of nature conservation were the immediate grounds for the conferring of knighthood in 1950; all rested, however, upon his life-long devotion to ecology.

Sir Arthur was internationally minded in science, and certainly did more than any one else of his generation to promote mutual understanding among scientists in his major field from different countries. His wish for close relations with America went beyond the bounds of science. I close this tribute with a quotation from a letter dated November 30, 1940, which is perhaps even more pertinent today than it was in the first year of World War I:

"I only hope, if and when we win through, your country and mine will have the sense and foresight to perceive that they must continue in the closest co-operation if there is to be any future for western civilization. . . . In a word we depend upon each other far too closely and vitally for forms of 'sovereignty' to matter in comparison with the danger of losing all that makes life worth living. We *must* stick together, and I only pray that our traditionalists—die-hard Tories here, isolationists with you—will not be able to prevent it. I am for the closest union that is any way practicable—and that is not a new view arrived at since this war began, but a conviction of long standing."

We are grateful that Sir Arthur lived and gave so abundantly to science and toward mutual understanding among men of diverse nations.

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AN EVALUATION OF THE ARMS-LENGTH RECTANGLE METHOD IN FOREST SAMPLING

INTRODUCTION

According to Cottam and Curtis (1956) the plotless methods of sampling are more efficient in terms of equipment needed and of results obtained per man-hour expended. In an attempt to develop a relatively rapid method requiring meager equipment, Rice and Penfound (1955) devised the augmented variable-radius method. This method utilized a combination of plotless (angle-gauge) and plot (arm-length transect) techniques. This report is a comparison of the results obtained by 60 arms-length rectangles with the results obtained by a complete census in a green ash bottomland forest, located in the Oliver Wildlife Preserve, near Norman, Oklahoma. Appreciation is expressed to D. C. Ahshapanek who participated in most of the field work. We wish also to thank D. W. Baepfer, R. A. Diener, Luis Freile, R. N. Sakamoto and V. E. Wiedeman for their help in collecting field data.

This community, described by Penfound (1948), is composed largely of green ash, *Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern. and the following secondary species: American elm, *Ulmus americana* L.; persimmon, *Diospyros virginiana* L.; cottonwood, *Populus Sargentii* Dode.; hackberry, *Celtis laevigata* Willd.; and bur oak, *Quercus macrocarpa* Michx. Since the study in 1948, drought conditions have prevailed in the Norman area, resulting in the death of many trees and a much more open stand. At the present time this forest comprises 145 living trees, 34 dead trees, and only 11 saplings per acre. The relatively high number of dead trees and the paucity of saplings (due probably to overgrazing) suggests that this forest is deteriorating rapidly.

METHOD

In the arms-length rectangle method, the only equipment required is a compass, a diameter tape, and a clipboard with appropriate data sheets. In practice, the worker first calculates the length of his pace and the spread of his outstretched arms. The worker then paces off, with arms outstretched, a distance equal to 0.01 acre along predetermined compass lines. While pacing off the imaginary rectangle, all tree species and diameters, at breast height, are announced and recorded by a companion. All species of saplings are recorded and shrubs may also be included, if desired. In this study 60 rectangles were utilized, distributed evenly throughout the 13.54 acre stand.

It should be noted that the length of one's pace varies with slope, obstructions, and other factors, and that the actual area of a given rectangle would only approximate 0.01 acre. Unless absolute values are imperative, however, the arms-length rectangle method is ideal since relative values can be calculated readily from the field data. Relative frequency is determined by dividing the frequency of a given species by the sum of the frequencies of all species. Relative density and relative basal area are calculated similarly. Perhaps the most important value is the importance percentage which is derived by adding relative frequency, relative density and relative basal area and dividing by three.

RESULTS AND DISCUSSION

A comparison of the relative data, as determined by the complete census and by the arms-length rectangle method, is presented in Table I. It will be observed that the relative frequencies of green ash and American elm are quite low when calculated by the census method. This diversity can be explained as follows: The area of the

squares utilized in the census (10,000 square feet) was much greater than that of the area of the rectangles (435.6 square feet). With the larger size of subsample the actual frequencies of abundant species increased less rapidly than those of the less common plants, resulting in lower relative frequencies for the more abundant species. This shift in relative frequencies demonstrates that even relative frequency is affected by the size of the subsamples. Except for American elm the relative densities and relative basal areas, by the arms-length rectangle method, were remarkably similar to the values derived by the complete census.

TABLE I. A comparison of relative frequency, relative density and relative basal area and importance percentage of species in a green ash forest near Norman, Oklahoma, according to the complete census and the arms-length rectangle methods

Species	FREQUENCY		DENSITY		BASAL AREA		IMPORTANCE PERCENTAGE	
	Census	Rectangle	Census	Rectangle	Census	Rectangle	Census	Rectangle
Green ash.....	23.06	38.17	54.79	51.18	43.59	38.79	40.49	42.05
American elm.....	17.97	25.53	13.39	21.26	15.75	19.55	15.70	22.11
Persimmon.....	17.97	19.15	19.53	15.75	5.50	3.70	14.33	12.87
Cottonwood.....	10.55	4.26	2.28	2.36	22.86	26.21	11.90	10.94
Hackberry.....	8.59	8.51	4.01	5.51	3.53	7.00	5.38	7.01
Bur oak.....	5.08	6.38	2.49	3.94	4.62	4.75	4.06	5.02
Others.....	16.78	None	3.51	None	4.15	None	8.14	None
Totals.....	100	100	100	100	100	100	100	100

The total area sampled by the arms-length rectangle method was 0.6 acre, which was only 4.4 percent of the area covered by the census. The total field time for the arms-length rectangle method was 6 man-hours as against 60 man-hours for the complete census. This method, therefore, results in a considerable saving in sampling time.

A total of 13 species occurred in the stand, whereas only six species were sampled by the rectangle method. It will be observed, however, that the total importance percentage of the infrequent species was negligible (Table I). Since the only species having more than 30 trees in the sample was the green ash (with 39 individuals) it appears that the total sample was minimal. Therefore, it is recommended that a sample of 100 arms-length rectangles of 0.01 acre each should be utilized for future analysis of forests of similar number of species and individuals.

SUMMARY

1. An evaluation of the arms-length rectangle method of forest analysis is presented. The standard of comparison was a complete census of a green ash bottomland forest with American elm, persimmon and cottonwood as important secondary species.

2. The method consisted of a series of 60 arms-length rectangles of 0.01 acre each, in which the DBH of all tree species and the list of all saplings were recorded. The comparison was made primarily on the basis of relative frequency, relative density, relative basal area and importance percentage.

3. Except for relative frequencies for the most abundant species, and the data on American elm, the values

obtained by the arms-length rectangle method approximated closely those obtained by the complete census.

4. In view of the meager equipment needed (compass, diameter tape and clip board) and the short time needed for sampling, this method is recommended for forest analysis.

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ALGAL AND LICHEN FLORAS IN RELATION TO NITROGEN CONTENT OF CERTAIN VOLCANIC AND ARID RANGE SOILS¹

This report evaluates alga- and lichen-stabilized surface crusts as nitrogen sources in soils from 13 volcanic areas in 5 western states and from typical range land of northeastern New Mexico. The study is an extension of an investigation of alga- and lichen-stabilized surface crusts as continually renewable sources of soil nitrogen in the Carrizozo, New Mexico, lava flow and the surrounding arid plain. It is based upon soil samples from a number of western volcanic areas and upon local range soils in northeastern New Mexico, which were being analyzed simultaneously.

METHODS

Samples, collected in the dried condition, in the field were placed directly on moist filter paper in sterile Petri dishes. A portion of each was dehydrated for the determination of amino nitrogen by Allen's method (1951) for semi-micro-Kjeldahl analysis. Total nitrite and nitrate determinations were made by a modification of Bray's procedure (Nelson et al., 1954).

The cultures were maintained in indirect light for several weeks for microscopic observation and the identification of algal and lichen species.²

The samples from volcanic sites were collected between June 16 and July 13, 1956, from the following locations:

State	Nearest town	Elevation
New Mexico	Capulin	6000'
Washington	Spokane	4000'
Oregon	Sand	800'
	Bend	4304'
	Lava Butte	4000'
	Crater Lake National Park	5000'
	Algoma	6000'
Idaho	Valley Falls, Abert's Rim	4309'
	Aberdeen, Crater of the Moon	3500'
	Rockford	3500'
California	Medicine Lake	6575'
	Lava Beds National Monument	6000'
	Shelly	4629'

All collections were made at random with no effort to select for algal or lichen growth. Of the 67 samples of volcanic soils, 15 were from depths of 2-4 inches, and 52

were from surface strata. Eighteen of the surface samples were alga-stabilized, and 12 were lichen-stabilized crust. The 55 range samples collected in northeastern New Mexico between March 1 and June 15 from the soil surface included 24 algal crusts.

OBSERVATIONS

Soil nitrogen content

Table I shows the averages of amino nitrogen and total nitrite and nitrate for the 122 samples from the various types of substrates lacking or supporting algae and/or lichens.

For volcanic soils, the amino nitrogen content of algal surface crusts was more than 4 times as high, and that of lichen crusts was more than 7 times that of similar samples lacking algae or lichens. The amino nitrogen of alga-stabilized surface crust on range soil was more than twice as high as in the absence of algae. The amino nitrogen of alga-stabilized crust averaged 41 per cent higher (2766 p.p.m.) and that of lichen crust 46 per cent higher (4312 p.p.m.) than for samples taken immediately below each type at depths of 4 to 6 inches. The amino nitrogen of surface crust supporting only moss was relatively low (806 p.p.m.), apparently because of the high cellulosic content of moss tissues.

The averages of total nitrite and nitrate for alga- or lichen-stabilized crust from volcanic areas ranged from around 2.5 to 6 times as high as at depths of 4 to 6 inches. Total nitrite and nitrate for volcanic soils averaged 2.3 times as high in algal crust and 1.6 times as high in lichen crust as in surface strata lacking such growth. For range soils, total nitrite and nitrate averaged 4 times as high in algal crusts as in surface layers lacking a photosynthetic microflora. The amino nitrogen of lichen crusts from lava soil averaged 36 per cent higher and the total nitrite and nitrate, 30 per cent lower than for the alga-stabilized stratum. For similar volcanic soil at Carrizozo, New Mexico, amino nitrogen of the lichen crusts averaged 22.2 per cent higher and total nitrite and nitrate 21.5 per cent lower than for the alga-stabilized stratum (Shields et al., 1957).

Alga and lichen floras

Average amino nitrogen, nitrite and nitrate were determined for both algal and lichen crusts containing each of the 7 species of algae found in this study on volcanic soils: *Microcoleus paludosus*, *M. vaginatus*, *Nostoc* spp., *Protococcus grevillei*, *Schizothrix californica*, *Scytonema hojmannii* and *Stichococcus subtilis* (Table II). Nitro-

¹ This investigation is one section of a study being subsidized by the National Science Foundation.

² The author is indebted to Dr. Francis Drouet, Chicago Museum of Natural History, for determinations of the algal species and to Dr. Grace Howard, University of Washington, for the lichen identifications.

TABLE I. Amino nitrogen, nitrite and nitrate for various types of volcanic substrates and for arid range land

Substrate	Number of samples	SURFACE		SUBSURFACE 4-6" BELOW SAMPLE ON LEFT	
		Av. amino N (p.p.m.)	Av. NO ₂ ⁻ NO ₃ ⁻ (p.p.m.)	Av. amino N (p.p.m.)	Av. NO ₂ ⁻ NO ₃ ⁻ (p.p.m.)
cinders	2 surface	151	0.56		
non-volcanic soil lacking algae, lichens or moss.	2 surface 1 subsurface	446	1.63	 263	 0.00
lava soil lacking algae, lichens or moss.	17 surface 7 subsurface	600	2.33	 419	 0.90
algal crust on lava soil.	18 surface 5 subsurface	2766	5.41	 1547	 1.91
lichen crust (some containing independent algal growth) on lava soil.	12 surface 2 subsurface	4312	3.78	 2312	 0.50
moss on lava soil.	1 surface	806	0.80		
range soil, New Mexico lacking algal or lichen growth.	31 surface	532	0.51		
algal crust on range soil, New Mexico.	24 surface	1260	2.16		
Total samples.....	122				

TABLE II. Average amino nitrogen, NO₂⁻, NO₃⁻ and incidence of algal species in stabilized surface crust of certain western volcanic and range soils

Algal species	Number algal samples and crust type	ALGAL CRUST		LICHEN CRUST	
		Av. amino Nitrogen (p.p.m.)	Av. NO ₂ ⁻ NO ₃ ⁻ (p.p.m.)	Av. amino Nitrogen (p.p.m.)	Av. NO ₂ ⁻ NO ₃ ⁻ (p.p.m.)
I. Volcanic soils from 5 western states:					
1. <i>Microcoleus paludosus</i> (Kutz.) Gom.....	3	2259	1.49		
2. <i>M. vaginatus</i> (Vauch.) Gom.....	16 (12 algal, 4 lichen)	2998	6.12	 4614	 3.12
3. <i>Nostoc</i>	3 (2 algal, 1 lichen)	2897	3.00	 4038	 2.80
4. <i>Protococcus grevillei</i> (Ag.) Crouan.	1	1560	5.10		
5. <i>Schizothrix californica</i> Dr.....	1	1560	5.10		
6. <i>Scytonema hofmannii</i> Ag.....	1	1322	1.04		
7. <i>Stichococcus subtilis</i> (Kutz.) Klerck.....	2 (1 algal, 1 lichen)	3641	6.16	 6514	 4.64
II. New Mexico range soils:					
1. <i>M. vaginatus</i> (Vauch.) Gom.....	16	1073	1.85		
2. <i>Porphyrosiphon fuscus</i> Gom.....	13	1491	2.54		

gen determinations were also made for range soil samples containing each of the 2 most common algal species, *Microcoleus vaginatus* and *Porphyrosiphon fuscus* (Table II). The algae listed for lichen crusts in Table II were isolated from the extra-lichen fraction of the sample. *Microcoleus vaginatus* was the most widely distributed species, appearing in 12 of the 18 alga-stabilized and in 4 of 12 lichen-stabilized crusts from lava soil and in 16 of 24 algal crusts among the 55 samples from range land. The predominance of *Microcoleus vaginatus* in volcanic substrates and on arid range soils is attributable in part to its pronounced resistance to desiccation. All species,

however, of 4 of the genera isolated, *Microcoleus*, *Porphyrosiphon*, *Schizothrix* and *Scytonema*, have gelatinous sheaths. *Porphyrosiphon fuscus* is prominent on range soil, being found in 13 of 24 algal crusts.

The soil lichens from the volcanic sites were predominantly *Cladonia chlorophaea* (Flk.) Spreng., *Diploschistes scruposus* (Schreb.) Norm. and *Lecidea decipiens* Ehrh. On volcanic soil at Carrizozo, New Mexico, the species occurring most frequently were *Dermatocarpon squamellum* (Nyl.) Herre, *Heppia despreauxii* (Mont.) Tuck. and *Collema coccophorum* Tuck. (Shields et al., 1957). The colorful displays of lichens observed

on basalt rock in the present study were mainly *Lecanora melanophthalma* (Lam. and D. C.) Ram., *L. rubinia* (Lam. and D.C.) Arch., *Candelariella vitellina* (Ehrh.) Mull. and *Physcia pulverulenta* (Schreb.) Hampe.

DISCUSSION

In 122 samples from volcanic and arid range soils the amino nitrogen of the alga- or lichen-stabilized surface crust constituted the bulk of total nitrogen in all cases where such crust was present. Averaging 2766 and 4312 p.p.m., respectively, for algal and lichen crusts from volcanic soils and 1260 p.p.m. for algal crusts from range soils, this amino nitrogen is mainly incorporated in living protoplasm. It is released upon the death of vegetative cells, resulting in a concentration of total nitrite and nitrate 1.6 to 4 times as high as in surface strata lacking a photosynthetic microflora. Since lichens and soil

algae persist during even extreme drought, the contribution of these organisms to total nitrogen is especially significant in arid soils.

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SUGAR MAPLE IN FOREST SUCCESSION AT WASHINGTON, D. C.

The status of sugar maple (*Acer saccharum*) in the upland climax forests of the Piedmont and Coastal Plain sections of Western Maryland has been evaluated by Chrysler (1910) and Shreve (1910). These authors stated that the chestnut-oak-hickory forests appeared to be the upland climax for these areas and that no evidence existed to indicate such forests might be replaced by others containing maple and beech—the characteristic climax species of uplands to the north and west. This statement was based upon three observations (Chrysler, 1910, p. 169): 1) the maple in the area was red maple, a lowland species, and not the upland sugar maple; 2) stands could not be found in which oak-hickory canopies had pronounced understories of maple and beech; and 3) the oldest tracts of upland forest to be found in the area consisted of chestnut, oaks, hickories and beech. This evaluation was largely substantiated by the publications reviewed by Braun (1950 and 1955) and the work of Hotchkiss and Stewart (1947). In the summer of 1955 the author conducted a vegetational survey of Rock Creek Park, located on the eastern edge of the Piedmont Plateau in Washington, D. C., and observed that both saplings and young trees of sugar maple were common in the area. Since the presence of this species in such numbers is contrary to published observations and data, it seems worthwhile to present these findings.

METHODS AND RESULTS

After preliminary observations showed sugar maple to be relatively common in Rock Creek Park, an attempt was made to locate suitable stands for quantitative sampling. Only one such stand, consisting of approximately 15 acres and located within the National Zoological Park southwest of the intersection of Klinge and Adams Mill Roads, was found suitable. This stand occurs on an outcrop of granitic-gneiss mica-schist; it has a slope of 10° to 25°, a southwestern exposure and a soil varying from a few inches to several feet in depth. In spite of its location within a highly populated area, the stand showed no evidences of trampling or other disturbances. This stand has been the property of the National Park Service for the past 67 years and has been protected by a high mesh fence for the past 42 years. There is no history of fire, grazing or cutting during its tenure with the National Park Service.

TABLE I. Composition of trees and saplings (3-12 in. circumference) in the National Zoological Park Forest. I.V. represents Importance Value

	TREES				SAPLINGS		
	Relative frequency	Relative density	Relative dominance	I. V.	Relative frequency	Relative density	I. V.
<i>Quercus alba</i> (white oak)	37.5	41.0	41.0	119.5			
<i>Fagus grandifolia</i> (beech)	26.5	24.2	15.7	66.4	27.1	39.7	100.2
<i>Quercus velutina</i> (black oak)	11.0	11.5	10.4	32.9			
<i>Quercus rubra</i> (red oak)	7.8	6.4	15.5	29.7	2.8	2.5	7.9
<i>Liriodendron tulipifera</i> (tuliptree)	6.2	7.8	14.3	28.3	1.4	1.6	4.5
<i>Quercus marilandica</i> (black jack oak)	1.5	1.2	1.4	4.1	1.4	0.8	3.3
<i>Frazinus americana</i> (white ash)	1.5	1.2	1.0	3.7	7.1	4.1	16.8
<i>Acer rubrum</i> (red maple)	1.5	1.2	0.2	3.0	10.0	9.9	29.9
<i>Acer saccharum</i> (sugar maple)	1.5	1.2	0.1	2.8	15.7	12.4	42.1
<i>Sassafras albidum</i> (sassafras)	1.5	1.2	0.1	2.8	2.8	1.6	6.6
<i>Carya cordiformis</i> (bitternut)	1.5	1.2	0.03	2.7	4.3	2.5	10.2
<i>Nyssa sylvatica</i> (tupelo)	1.5	1.2	0.01	2.7	4.3	4.1	12.6
<i>Cornus florida</i> (flowering dogwood)					8.5	8.2	25.0
<i>Carpinus caroliniana</i> (hornbeam)					4.3	5.0	14.0
<i>Prunus serotina</i> (wild black cherry)					5.7	3.3	13.5
<i>Cercis canadensis</i> (red bud)					1.4	2.5	5.8
<i>Liquidambar styraciflua</i> .. (sweet gum)					1.4	0.8	3.3
<i>Tilia americana</i> (basswood)					1.4	0.8	3.3

The trees were sampled by the random pairs method (Cottam and Curtis 1949) using an exclusion angle of 160° and a total of forty points (eighty trees). Saplings, considered here to be any woody stem with a circumference between three and twelve inches, were sampled for frequency and density by taking the four closest saplings to each point in the random pairs survey. The stand was found to be homogeneous according to the criteria established by Curtis and McIntosh (1951).

The composition of the trees and saplings occurring in the stand is given in Table I. The relative frequencies, relative densities, relative dominances and importance values (I.V.) for the trees were computed according to methods devised by Curtis and McIntosh (1951). Since the sapling data did not include dominance values, the importance values for saplings were calculated by the formula

$$I.V. = \text{relative density} + \text{relative frequency} \times 1.5$$

(Whitford and Salamun 1954) so that the importance values for the trees and saplings would be directly comparable. The distribution of trees by basal area size classes is given in Table II. Taxonomic nomenclature is according to Fernald (1950).

TABLE II. Distribution of trees by basal area size classes; number of individuals in a sample of 80 trees

Square inches:...	12-50	51-100	101-150	151-200	201-300	301-400	401-600	601-800	801-...
<i>Quercus alba</i>	..	9	2	4	11	2	3	..	1
<i>Fagus grandifolia</i>	5	..	6	3	3	..	2	..	..
<i>Quercus velutina</i>	..	..	1	2	5	1	..	..	..
<i>Quercus rubra</i>	..	..	..	..	..	2	..	2	1
<i>Liriodendron tulipifera</i> ..	..	..	..	1	..	2	..	3	..
<i>Quercus marilandica</i>	..	..	..	..	1	..	..	..	..
<i>Frazinus americana</i>	..	..	..	1	..	..	..	..	..
<i>Acer rubrum</i>	1	..	..	..	..	..	..	..	..
<i>Acer saccharum</i>	1	..	..	..	..	..	..	..	..
<i>Sassafras albidum</i>	1	..	..	..	..	..	..	..	..
<i>Carya cordiformis</i>	1	..	..	..	..	..	..	..	..
<i>Nyssa sylvatica</i>	1	..	..	..	..	..	..	..	..

DISCUSSION

A sapling stratum composed of more tolerant species than the canopy and an absence or paucity of canopy species in the sapling stratum indicates that succession is still operative in a stand. From Table I it would appear that this stand is not in a climax condition, since only one of the first five leading dominants has a higher importance value in the sapling stratum than in the canopy. Two of the canopy species (white oak and black oak) do not appear in the sapling layer, while two other species (red oak and tuliptree) are present in only small amounts. Of the leading dominants, only beech is significantly represented in the sapling stratum. Further, an inspection of Table II indicates that white oak, black oak, red oak and tuliptree have been unable to mature saplings in this stand for some time, since trees of these species are not present with basal areas of less than 50 square inches. White oak, although clearly the dominant species of the stand at present, appears not to be reproducing itself and in the future, as the older trees die, its replacement in the canopy will be accomplished by species whose saplings and seedlings have been able to survive under the oak canopy. A similar statement could also be made for black oak, red oak and tuliptree. The sap-

lings of beech, however, are doing well under the present canopy and this species might be expected to remain in the canopy.

If the future canopy composition of a forest stand is dependent upon the present sapling stratum, then the future dominants of this stand can be predicted to be beech and sugar maple. Both of these are climax species throughout their ranges and there is no reason to believe they will behave otherwise here. As the saplings of these two species grow to tree size, the shade within the forest will increase, thereby rendering the environment less favorable for the reproduction of intolerant species (i.e., white oak, black oak, red oak and tuliptree) and more favorable for the reproduction of beech and sugar maple. It seems likely, therefore, that beech and sugar maple will increase in importance in the sapling and seedling strata as well as in the canopy.

Although ranking fourth in I.V. for saplings, the understory small tree *Cornus florida* is not capable of reaching the canopy stratum. Since this species is known to be a component of climax stands elsewhere (Braun 1950) it is likely to remain in the stand. *Cercis canadensis*, another small tree species, can be expected to behave in a similar manner.

Red maple and white ash are considered to be intermediate in tolerance. The increase in I.V. for saplings over trees indicates that these species will remain in the stand and are likely to become the third and fourth ranked species. Of the remaining trees, based upon their behavior elsewhere and their I.V. for both trees and saplings in this stand, *Carya cordiformis*, *Nyssa sylvatica*, *Carpinus caroliniana* and *Tilia americana* seem likely to remain in the stand, while *Sassafras albidum*, *Prunus serotina*, *Quercus marilandica* and *Liquidambar styraciflua* are likely to disappear from the stand.

The stand examined in the present study is in apparent contrast with the composition of upland climax forests in this area as evaluated by Chrysler (1910 p. 169) in that: 1) sugar maple, as well as red maple, is present in sufficient numbers in this general area to be considered as a possible dominant in upland forests; 2) the pronounced understory of beech and sugar maple (more than one-half of the saplings) and the paucity of oak, hickory and tuliptree reproduction indicate that these latter species will be replaced by beech and sugar maple as succession progresses; and 3) the composition of the "oldest stands," as admitted by Chrysler, does not necessarily represent the composition of the primeval forests. Further, these primeval forests, if considered to be the forest composition at the time white man first appeared in America, were not necessarily in the climax state (Day 1953).

Two suggestions may be advanced to account for the discrepancy between the status of sugar maple in this stand and the observations of Chrysler and Shreve. Firstly, the elimination of chestnut (*Castanea dentata*) by disease from the area may have altered the interrelationships among the component species of these forests in a manner favorable to sugar maple. Braun (1950, p. 192), however, suggests that it is too early to evaluate these adjustments: "... the replacement of chestnut by oaks seems to be taking place in many sites; in some the tuliptree has increased; in others, more mesic and shade-tolerant species appear to be favored. ... only after several generations of forests could an equilibrium be reached, and the dominants of the new climax be determined." Secondly, much of the area in and around the District of Columbia has been removed from agricultural

use during the past fifty years and, with increased urbanization, many isolated stands have received increased protection from grazing and fire, and thereby more favorable conditions for the growth and reproduction of the mesophytic sugar maple undoubtedly have been created. If either or both of these suggestions be true, other sites in the Piedmont and Coastal Plain areas of the Middle-Atlantic States with long records of protection from fire and grazing should be examined for evidences of recent increases in the amount of sugar maple in the seedling, sapling and young tree age classes.

SUMMARY

A vegetational survey of Rock Creek Park, located on the eastern edge of the Piedmont Plateau in Washington, D. C., indicated that sugar maple is relatively common in the area. Since this was contrary to published observations and data a stand within the Park was quantitatively sampled. The obtained data indicates that sugar maple is increasing in importance in this stand and it is suggested, based upon sapling reproduction data, that in the future sugar maple will become a dominant in the stand.

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REVIEWS

GENERAL SYSTEMS¹

It has become painfully clear that the future progress of ecology is going to depend on developing theoretical tools of high complexity and precision. Typically, in any living science, a period of concept formation is followed by a longer interval during which data accumulation proceeds to the point of almost, but not quite, complete chaos. Then a new period of concept formation intervenes.

During the process of realigning the theoretical superstructure with the factual content of a science, intellectual contributions are offered by a variety of self-appointed saviors. This process is necessary, but dangerous, since, at the present stage of development in ecology, well-meaning naïve intelligence is not a trustworthy source of a new fundamental philosophy. In fact, no man who cannot clearly distinguish between scientific philosophy and philosophical speculation, should be permitted to do either one. What is required is that minds trained in mathematics, logic, philosophy, and the subject matter of at least one empirical discipline must consciously examine the more difficult problems in each field and restate them in such a way as to make their solution at least theoretically possible. In the process it will be discovered, in ecology, that many of the problems which have been the center of polemical literature are actually pseudo-problems, will-of-the-wisps exhaled from tangled verbiage.

The job of the professional theoretician will be especially valuable to the extent that he brings to bear on a problem in one discipline the logical techniques which have been shown to be fruitful in dealing with a formally identical problem in another discipline. Eventually it can be hoped that vast areas of biological and social science will be found to be underlain by a few broad formal structures. Consider the possible example—that the problem of community dynamics may be logically identical with the problem of balanced national economy.

Careful logical analysis, concern with pattern and formalism, and emphasis on relations between diverse dis-

ciplines are the core of General Systems Theory. It is a tremendous dream and there may be enough Platonism left in nature for part of the dream to be true.

General Systems Theory is primarily a way of examining natural phenomena, rather than being a body of scientific information in the usual sense. The General Systems Theorist is not the same as a mathematical or statistical consultant but is actually an empirical scientist, better trained than most in the techniques of theory construction.

The Society for the Advancement of General Systems Theory has published, as its first yearbook, a sampler of papers in the biological and social sciences which demonstrate the power of the General Systems approach.

All these papers have previously appeared elsewhere; but it is important to read the collection as a collection, since the yearbook is a fairly complete definition of General Systems Theory. When the concept is understood, I am certain that applications to ecological problems will become obvious to most readers.

Do not be frightened by complexity of notation or terminology. Each paper is complete in itself and a concept which is left obscure by one author may be clearly stated by another. Some of the non-biologist authors have unfortunate pieces of half-knowledge about biology. Do not be unduly disturbed. What is significant is the method of reasoning rather than the empirical subject matter.

Ecology could profit from the intellectual rigor and courage employed by the authors in the yearbook. This courage does not mean racing wildly off into pseudo-ethical speculation on the slightest shred of evidence, but rather seeing the clean outlines of a problem as it exists, despite the twin menaces of pedantic caution and missionary zeal. Rigor involves treating the empirical data with the firm precision one uses to remove a splinter from a child's hand.

A solid theoretical foundation is necessary if ecology is to make orderly progress. The General Systems approach may help. It certainly cannot add any significant amount of confusion.

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FUNDAMENTALS OF PLANT DISTRIBUTION AND VEGETATION STUDY¹

The able European geobotanist Prof. H. Walter is surveying in his *INTRODUCTION TO PLANT SCIENCE* the

¹ Walter, Heinrich. *Einführung in die Phytologie*. III. *Grundlagen der Pflanzenverbreitung*. I Teil. *Standortslehre (analytisch-ökologische Geobotanik)*. 525 pp., 73 figs. 1951. 29.80 DM (\$7.10). II Teil. *Arceuthamnologie (floristisch-historische Geobotanik)*. 246 pp., 216 figs. 1954. 16.20 DM (\$3.90). IV. *Grundlagen der Vegetationsgliederung*. I Teil. *Heinz Ellenberg. Aufgaben und Methoden der Vegetationskunde*. 136 pp., 19 figs. & 21 tables. 1956. 9.40 DM (\$2.25). Stuttgart: Eugen Ulmer.

field of botany. The first two volumes have dealt with the life of plants in general (3rd ed., 1950) and plant classification (2nd ed., 1952). The three volumes reviewed here,¹ plus a future one to systematically consider the vegetation of central Europe, cover our American "plant ecology." They treat the ecology, chorology, and history of plants, and begin the study of vegetation in Prof. Ellenberg's volume.

The plant life of Germany is the focus for Walter's work, but few men can have had such wide botanical experience as he. He has ranged in Europe from the Ukraine to Lapland and included the Mediterranean and

Near East, southern Africa, and the American Southwest.

In the large volume on the study of environment (III, Part I), Walter considers the plant with its environment as a unit. Indeed, this viewpoint differentiates for him ecology from physiology. Both studies can be experimental and quantitative. The abundant quantitative data in the book result from suitable choice of definitions and apparatus. Such data mark the maturation of ecology and lend to the subject a universality impossible to attain in any other way.

Habitat conditions are treated under factors which act directly on plants: heat, water, light, chemical factors, and mechanical factors. Space is allotted in ratios of 10:23:7:9:3. Many of Walter's discussions are of particular interest because of content, excellence, omissions, placement, or emphasis. Different levels of climate, such as regional, local, and microclimates, are discussed under the heat factor; and ecotypes are considered here because the work of the Carnegie group in California provides most of the illustrative material. The Carnegie data really are concerned with plant responses to different temperature regimes.

The section on water relations of plants is large and detailed, in correspondence with Walter's interests over many years. The soil moisture review is excellent, but rather strange to us with our emphasis on permanent wilting point and field capacity, as determined with pressure membranes, and our lack of correlation between osmotic pressures generated by roots and the corresponding soil water tensions at wilting. Transpiration is measured by short-period weighing of cut branches. The theoretical objections against this method are numerous. They are of doubtful validity, and the method is a standard one in European ecological research. For those interested in the biology of particular species, osmotic pressures, transpiration amounts, and quantitative data on assimilation are tabulated.

Under chemical factors is an excellent introduction to soils and their ecology. Those human structures, cultivated soils, are not neglected. The section on lime-plants and pH uses ideas of *bodenwag* and *bodenstet* with stenotopic and eurytopic to give a balanced presentation. Biotypes or other taxa behave as individuals, and adjectives such as these can be used to individualize their soil relationships. As a culmination of many lines of investigation, Schimper's theory of physiological drought of acid and cold soils is laid to rest.

The volume on chorology and history (III, Part II) treats first the nature of plant distribution areas. Kinds of areas, their extent, form and centers, shifts in kind of biotope occupied by a species when comparing one part of its area with another, and the major floristic regions of the world are compressed into fifty pages. This is possible partly because of Meusel's² earlier work. Meusel systematically considered methods of showing plant distribution on a map, local mapping, and sources of distribution maps. He compiled and made sense out of data on the relations of distribution areas to single ecological factors and to plants' history. Meusel's logic was impeccable and devastating for causal ecology of a regional, observational kind. Ecologically we can often describe areas, including their limits, but we cannot often explain them. In historical plant geography Meusel worked back in time from present means of dispersal to

historical times, to postglacial times, and to the Tertiary. Interpretations of present areas solely on a "historical" basis he rightly considered highly hypothetical. Meusel concluded then that a profitable way of regarding plant distribution areas is as *Gestalt* phenomena. Types of distribution areas can be abstracted. These types, and the more or less ecologically or historically conditioned, equiformally progressive areas of species belonging to these types, Meusel regarded as an improvement over the older plant-geographical idea of floristic elements. Meusel's concepts require a more exact factual basis, and this he helps to provide in his volume 2. An index listing about 3500 species makes his data instantly available, while some 700 references indicate the adequacy of literature coverage.

Walter's volume on distributions next presents a plant-geographical, paleobotanical history of the earth's vegetation since the Carboniferous. The detail increases tremendously as the present is approached. In less than ten pages we are in the Tertiary, with a well-balanced presentation of the need for continental drift behind us. The Tertiary is treated in some detail and the Pleistocene in more. This is quite in contrast to the now excellently known Tertiary history of the western American floras, where the Pleistocene is lumped. A chapter on present disjuncts, which maps today's distributions with those paleobotanically known, gives one more confidence that present areas can allow conclusions about those past distributions for which paleobotanical data are lacking. Post-glacial time leads into a presentation of pollen analysis' role in so beautifully unraveling the forest history of central Europe. Finally, historical forest changes in central Europe are discussed. Here again pollen analysis offers data on natural or original conditions and on the influences exerted by early man. Written evidence continues the story, and the conclusions from it all bear directly on any theories of climax vegetation.

Geographic elements of floras are the next topic. The focus is quickly narrowed from a global (following Good), to a Eurosiberian, to a European compass. Many distribution maps, lists of species (with ecological notes) illustrate the Arctic floristic region (tundra zone), the Boreal floristic region (conifer zone), the central European (broad-leaved forest), Atlantic (dwarf-shrub heath), Mediterranean (sclerophyll), Pontic (steppe), southern Siberian (open birch forest), Turanian (Aral-Caspian semi-desert). Here is no conflict between floristic and vegetational views of the plant cover. Ecology and chorology are combined in the discussion, although Walter is careful to point out that all the plants of a floristic zone do not have the same ecology. Walter has shown once more how valuable floristic plant geography is to ecology.

In the volumes discussed above Walter has laid a foundation for the study of vegetation. The subsequent volume, *THE BASIS OF VEGETATION ORGANIZATION* (IV, Part I), is by H. Ellenberg, who has worked with both Walter and Tüxen, and from their and his views achieves a most interesting synthesis.

Ellenberg discusses the many ways of studying vegetation—descriptively, systematically, ecologically, experimentally, dynamically, chorologically by both floristics and cartography, and as an applied study. Some kind of stand survey (*Aufnahme, relèvé*) must be the raw material for any of these treatments. It is the raw material which can be ordered under a given viewpoint. In describing stands, Braun-Blanquet's estimate methods are used, with additions.

² Meusel, H. 1943. *Vergleichende Arealkunde*. Berlin: Borntraeger. Vol. 1, xii + 466 pp. Vol. 2, xii + 92 pp. of lists + 90 pp. of maps.

Basic to all study of vegetation and the ordering of stand surveys are Ellenberg's conclusions that, when many stand surveys have been made, one realizes: 1) the same combinations of species occur many times in places often widely separated spatially, 2) no two stand surveys are exactly the same, 3) there are continuous variations between stand surveys. Ellenberg also discusses other recurrent questions of vegetation study, such as concrete and abstract communities, organismic nature of stands or combinations of individuals, species and ecotypes as ecological units, competition.

Some system will be applied to the stand surveys taken. They will be ordered and organized; and vegetation units, continua, gradients, sequences, or functions will be abstracted. Evidently based on his above-mentioned empirical and theoretical conclusions, Ellenberg presents step-by-step the technique used in Braun-Blanquet's system of vegetation study based on characteristic and differential-species. This technique of tabular processing of stand samples or surveys to detect diagnostic species and to compare stands can be learned. Ellenberg spells it out in detail and with great clarity. It seems to deserve trial on North American vegetation. Ellenberg's presentation of the system and its technique is more effective than that in the basic text, Braun-Blanquet's *PFLANZENSOZIOLOGIE*. Ellenberg assumes less prior knowledge and botanical experience on the part of the reader, and he makes a highly successful effort to simplify the presentation. However, he does take for granted an acquaintance with the amplified accounts of concepts and methodology in the second edition (1951) of *PFLANZENSOZIOLOGIE*.

Besides this tabular comparison of stands as a means to arrange like vegetation with like, Ellenberg presents methods of establishing vegetation units based on mathematical calculations of similarities, on ecological groups, on types of plant distribution areas, and on succession. The problematic nature of the evidence usually produced in support of the last is emphasized. Plant distribution areas refer primarily to floras; they refer to vegetation differences alone only so far as these are a function of floristic differences alone. The other methods of mathematical correlation and ecological groups also use or substantiate the first method of tabular comparison of vegetation stands.

A section on mapping vegetation is followed by the concluding part on "causal vegetation science." By this Ellenberg means quantitative methods of measurement combined with experiment. Competition receives some of the attention it deserves, and in a most stimulating way. Ellenberg has studied experimentally the difference between "physiological" and "ecological" behavior of plants. The first refers to growth in pure stands, the second to growth in natural, mixed stands. Shifts in tolerance optima for specific factors, or even breaks in the continuity of tolerance for a factor, may result from competition.

This series of books deserves the attention of all plant ecologists. It covers from an ecological viewpoint the life and classification, the autecology, distribution, and history of plants, and their community relationships.

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SNOW-BED VEGETATION¹

Where plants grow under extreme conditions, one ecological factor is generally so predominant that there is a comparatively simple correlation between the variations of this factor, and the reactions of the plant communities. Such single-factor vegetation has, because of its inherent simplicity, always been a favorite study object of synecologists: alpine, desert, water, etc. vegetation has been much more extensively studied than the mesotrophic communities, where the interplay of factors is much more difficult to analyze.

One of the most extreme sets of conditions under which plants may grow are those of the *snow-beds*. In the alpine and arctic regions winter snows do not cover the ground to the same depth everywhere: small depressions are filled with snow, ridges are blown free of snow. Through vortex formations, small initial differences of level may increase, and the snow builds up to great depths in some places. In other places, the bare ground projects through the snow.

Insufficient snow-cover is detrimental to vegetation: winter snow protects against too low temperatures and, what is more important, against the desiccating and abrading effects of winter storms. On the other hand a too long-lasting snow-cover will cut away from the precious few summer days during which plants can grow

and flower. Thus, a medium snow-cover will in each altitude belt correspond to an optimal plant community, which may be a low cope in the uppermost part of the sub-alpine region, or, e.g. a *Vaccinium myrtillus* community higher up in the alpine region.

Places with much more snow than this medium, optimum quantity form the *snow-beds*, which have been extensively studied by Scandinavian botanists for the last 55 years. Duration of snow-cover, character of bed-rock, and quantity of available moisture are the three dominating factors in mountain vegetation research, and, of these, the snow-cover is generally the one of greatest physiognomic importance.

Through the studies of different authors, especially through Nordhagen's two monumental vegetation monographs from Sylene (1928) and Sikilsdalen (1943), and, even more, through his admirable synthesis of Scandinavian mountain vegetation (1936) we knew a great deal about the snow-bed plant communities on hard, acid rocks in the South Scandinavian mountains. Conditions in the North were less well known, and those on limestones and mica schists were not properly understood.

The present paper—which was preceded by a more detailed study of a hard-rock mountain massif—remedies the situation: The author has covered the major part of the Scandinavian peninsula, and he has also managed to sort out the much richer and more complicated communities on "good" rocks. It represents the results of 11 years' studies in the field. The extreme western mountains, which are characterized by excessive quantities of

¹ Gjærevoll, Olav. 1956. The plant communities of the Scandinavian alpine snow-beds. K. Norske Videnskabers Selskab, Trondheim, Skrifter 1956(1): 1-405, 80 figs. Trondheim: F. Bruns Bokhandel. N. Kr. 40,00, \$5.60.

snow, are not adequately represented, otherwise the coverage seems to be very good.

As indicated in the title, alpine region snow-beds have been the object of Gjærevoll's investigation. This means that we get no account of the sub-alpine snow-beds, those chionophilous communities which are found below the timber-line, e.g. the sub-alpine *Nardus stricta* grass heaths (while the alpine ones are beautifully represented). On the other hand, the account of the alpine snow-beds is of an almost unheard-of completeness. Plant communities have been analyzed for composition by the methods of the Scandinavian school of phytosociology. Tables give the composition of almost 1800 (m² or 1/4 m²) quadrats, and more than 500 pH measurements are quoted. It should also be remembered that part of this material has been collected in rather far-off-the-track places, where it has been necessary to carry everything, provisions, tents, etc. on the back. The work therefore also represents a very great physical achievement.

With duration of snow-cover as the primary ecological factor, humidity and soil reaction come in as secondary ones. Some snow-beds dry out later in summer when all snow has melted. Others are situated below permanent snow, and kept moist by percolating meltwater, or they form part of water-courses and are kept moist that way. This, then, gives the foundation for a sub-division of snow-bed plant communities, the main features of which are quoted below. All the plant communities (alliances) mentioned below are generalizations of a number of

communities of lower rank (sociations) dealt with in the statistical tables.

Where snow melts extremely late, the growth season is too short for higher plants, the soil is practically always moist, and we get the two alliances *Polytrichion norvegici* on hard rock, *Distichion capillacei* on calciferous rocks. In less extreme snow-beds we also find a difference between the drier and more humid communities: *Herbaceon* (dry) and *Stellaro-Oxyrion* on hard rock, *Polarion* (dry) and *Oppositifolio-Oxyrion* on calciferous ones. In even less extreme communities we find a similar series: *Deschampsio-Anthoxanthion* (dry) and *Ranunculo-Anthoxanthion* on hard rock, *Reticulato-Poion alpinae* and *Ranunculo-Poion alpinae* on calciferous ones. To these adds itself one specialized community on hard rock: *Cryptogrammo-Athyrium alpestre* which occurs where the ground consists of comparatively big boulders, between which the two ferns grow. This alliance is partly also found at somewhat longer snow-cover than the one characterizing the last-mentioned group.

For the composition of the individual plant communities reference must be made to the original publication. Because of the great number of species common to arctic-alpine habitats in both hemispheres, the publication is of importance far outside of Scandinavia—where it will in the future be difficult to find a snow-bed community not already treated by Gjærevoll.

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THE HISTORY OF NORWEGIAN VEGETATION¹

Pollen analysis was conceived in the transitional area between the middle-European deciduous forests, dominated by oak and beech, and the northern area of coniferous forest, dominated by pine and spruce. Within this transitional area—of many hundred kilometres' extension—minor factors of habitat and micro-climate decide whether the elements of the southern or the northern vegetation type shall dominate. Small climatic changes are sufficient to upset all those sensitive equilibria and cause the elements of one or the other type to extend their area at the cost of those of the opposite one. As long as we are sufficiently far south so that the elements of deciduous forest never were absent, even under unfavorable conditions, and so far north that those of the conifer forest did not disappear totally even during the most favorable situation, we have the ideal conditions for analyzing climatic events by means of pollen analysis, especially if the elements of both vegetation types are few and easily recognized.

Such conditions prevail in middle Sweden where von Post, did his pioneer work 40-50 years ago, and similar conditions also prevail in southern Norway, which has been neglected by pollen analysts until recently. In his paper about conditions at the head of the Oslofjord Hafsten has definitely placed southeastern Norway on the pollen-analytic map.

The localities are all situated inside the so-called Ra

¹ Hafsten, Ulf. 1956. Pollen-analytic investigations on the late Quaternary development in the inner Oslofjord area. Universitet i Bergen, Arbok 1956. Naturvitenskapelig rekke nr. 8: 1-161 pp., 16 pl. (29 pollen diagrams). N. Kr. 15,00, \$2.10.

line, i.e. inside the moraines of the last major glacial advance. Consequently, one cannot expect his material to show any Late-Glacial development. But with the onset of more genial conditions at the beginning of the Post-Glacial, the ice receded from the area; and a vegetational development was started which, on the whole corresponds with that from adjacent areas in the east, south, and west. The classical division into five periods—Pre-Boreal, Boreal, Atlantic, Sub-Boreal, and Sub-Atlantic—is very distinct.

As a marked marine regression has taken place, the oldest strata are only found in basins situated above 150 m altitude, and not in all of them either. The isolation of a basin from the sea is generally marked by a maximum of *Hippophaë*-pollen, which is very great in some of these basins, 16 or 19%. The Pre-Boreal pollen diagram is very poor, being chiefly dominated by *Pinus* and *Betula*. In the usual way, the transition to the following period is marked by the appearance of *Corylus*, which never reaches high values—maximum generally ca. 20% or less.

As usually, the appearance of *Alnus* pollen marks the transition to the following two periods, during which takes place the usual immigration of and shift of dominance between *Ulmus*, *Tilia*, and *Quercus*. During the latter part of the Sub-Boreal period *Picea* immigrates and establishes itself at the transition to the last period.

The influence of agriculture is first noticed at the beginning of the Sub-Boreal period, not much later than its introduction in Denmark. *Plantago lanceolata* is the most important indicator of land clearing and agriculture. Later agricultural phases manifest themselves in the

diagrams. Pollen grains of *Linum catitissimum* should be mentioned among the "Cultivation pollen."

The movement of the shore-line can be followed from ca. 220 m—which coincides with the previously known maximum level—to the present-day level in a continuous sinking with decreasing speed, but without any breaks because of secondary transgressions.

Most important is perhaps the methodological part of the work. Papers have been published with a greater number of diagrams. Papers have also been published in which a diagram has been more carefully elaborated. But no paper has so far been published in which such a great material has been dealt with so carefully. Arboreal pollen spectra are based upon more than 500 grains, to which are added the non-arboreal pollen. Besides the ordinary arboreal diagram, there is a special diagram of the thermophilous elements, one total diagram, and a separate diagram of non-arboreal pollen.

This very careful method of working has permitted the author to push his enquiry far beyond the reaches of classical pollen analysis, and to elucidate the history of certain floristic elements not forming a regular part of the forest vegetation. It is thus interesting that, even if his area was not laid bare from ice until the beginning of the Post-Glacial period, and even if a forest vegetation followed immediately upon the recession of the ice, the author could show that some of the very interesting ele-

ments of the Late-Glacial park tundra flora have penetrated into the area, and have been able to maintain themselves there much longer than on the plains of Denmark or Middle Europe. The most interesting of these plants is represented by the find of pollen grains of *Sphedra cf. distachya* even in deposits from the Atlantic period. If we accept the view that the Late-Glacial park tundra elements were, above all, heliophilous, it is easily conceivable that they could maintain themselves in suitable localities, e.g. steep rocks, long after they had been shaded out by the closing forests of the plains.

Finds of *Viscum album* and *Hedera helix* pollen shows that these species, which do not now go quite as far north as Oslo, did so previously. Most astonishing in this respect is a diagram from outside (ca. 100 km north of) the proper area of investigation: both *Viscum*, *Hedera*, and even *Ilex aquifolium* were represented by pollen finds there. Especially the *Ilex* pollen grain is very important: it would indicate that winter temperatures were then something like 6° C higher than they are now. Similar indications are given by the other finds mentioned, but the difference between then and now was not necessarily quite as great.

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FORESTS OF THE WORLD¹

A summary of the distribution, nature, quantity, quality, and uses of the world's forests presented between the covers of a single book is the objective of a compendium sponsored by the American Geographical Society and edited for them by Stephen Haden-Guest, John K. Wright, and Eileen M. Teclaff. Actually, this book represents the second attempt by Americans to bring world forest data together; the first being a book by Zon and Sparhawk² which has proved of great value, but which has been long out of print. As such, it is a timely and worthwhile effort, and one which will be needed and consulted frequently by the ecologist.

The thirty-one chapters are the work of some thirty-five forestry experts, garnered from all over the world. Therein lies both the outstanding strength and the weakness of the book. There is little uniformity of purpose or style; most of the chapters could just as well have appeared separately in a semi-popular journal. At the same time, many of the writers are the obvious authorities on their particular geographical area, and what they say is important and valuable.

The book is divided into three sections: (1) General, (2) Regional, and (3) The Outlook. The first consists of five chapters and 111 pages. It is essentially a very elementary textbook on forests and forestry. The authors—Paul B. Sears, Wendell H. Camp, Samuel T. Dana, J. W. B. Sissam, and George M. Hunt—are both authorities and competent writers, but the whole section suffers

from the obvious limitations imposed on any effort to compress a series of major subjects covering the world into a few pages, and the resulting product seems out of place in view of the avowed objectives of the entire work.

It is the series of 25 chapters detailing the forest resources of the world's forest regions that constitute the intrinsic worth of the book. Some of these sections are exceedingly valuable; but others are brief, general, and reflect the particular interests of the writer. All provide generalized descriptions of the major vegetation regions, names of the key timber species, and remarks on the economy and forest products industries. In a few cases, especially for Canada and the United States, recent statistics concerning the forests are summarized; but the availability of such data varies widely from place to place, and there is little consistency in the choice of what is presented. The very fact, though, that a substantial number of the articles are prepared under the signature of men who hold key forestry positions in their respective countries makes the assemblage worthy of careful study and reflection.

The final section consists of a single chapter by Erhard Rostlund of the University of California on the outlook for the world's forests and their chief products. Well written, the chapter takes a middle view of the future, balancing the long-time trend of forest devastation against the evolution of modern forest management and the "half-promise" of technology. The book thus ends on a note of competence and judgment.

In summary: a most valuable addition to the literature of dealing with forests and forestry, somewhat marred by unevenness in treatment and lack of uniformity of purpose between the many authors.

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¹ Haden-Guest, Stephen, John K. Wright, and Eileen M. Teclaff, Editors. 1956. A world geography of forest resources. American Geographical Soc. Special Publ. 33, xviii + 736 pp., illus. New York: Ronald Press Co. \$12.50.

² Zon, Raphael and William N. Sparhawk. 1923. Forest Resources of the World. 2 vol. New York: McGraw-Hill Book Co.

THE NEW SOVIET VEGETATION MAPS¹

Never has a vegetation map of so large an area been made at so large a scale as the new vegetation maps of the Soviet Union at 1:4,000,000. They may therefore be considered a milestone in the history of vegetation mapping, and deserve attention.

This monumental work has been completed by the staff of the Geobotanical Institute of the Academy of Sciences of the U.S.S.R. (Leningrad, 1955) with the collaboration of scientists all over the country, under the able leadership of E. M. Lavrenko and V. B. Sochava. These two men acted as editors and as contributing authors, and rightly so, for they are today the Soviet Union's leading authorities in the field of vegetation mapping.

What a challenge to map the vegetation of an area more than two and three quarter times the size of the United States! How gratifying to see such a vast research program crowned with real success.

Much cartographic material on the vegetation of the U.S.S.R. had accumulated, and a solid foundation been laid. However, most readers will find it hard to appreciate the disheartening difficulties the map editors must overcome in compiling a vegetation map of so large an area. Particularly the task of coordinating and integrating the available material into a harmonious unit requires great skill and patience, when amount, purpose and quality of the source material must necessarily vary enormously.

Wonders never cease, and in this case the astonishing feature lies in the fact that two different maps (of 96 x 69") were printed instead of one. Considering the high printing cost of large, complex, colored maps, such a feat is all but impossible in a capitalist country. Both maps are elaborately colored, and both are at 1:4,000,000; they are entitled VEGETATION MAP OF THE U.S.S.R. and GEBOTANICAL MAP OF THE U.S.S.R. respectively.

The VEGETATION MAP is the simpler of the two. It has 67 legend items, of which 12 are further subdivided. The arrangement of the map content is by vegetation zones, and the description of the vegetation is physiognomic, e.g. bunch-grass steppes. Frequently legend items have strong ecological implications, such as solonchak meadows. Regional terms like "Kolchic" are also used, but perhaps their function seems to be more that of an aid to locating them on the map rather than describing the character of the vegetation. Generic or specific names occur; they, too, serve to describe the physiognomy of the vegetation rather than the floristic composition (for example: grass-*Artemisia* semi-desert).

In contrast to the VEGETATION MAP, the GEBOTANICAL MAP OF THE U.S.S.R. dwells heavily on floristic descrip-

tion. It is more detailed, having 109 legend items, of which 46 are further subdivided. Counting the subdivisions as individual vegetation units, the GEBOTANICAL MAP has 210 items as compared with 87 items on the VEGETATION MAP. Both maps are further enriched by small black symbols which may stand for a species or a vegetation type. Sometimes a symbol refers to a given species in one region and to another species (of the same genus) elsewhere, e.g. *Fagus sylvatica* (Carpathians), *F. taurica* (Moldavia, Podolia), *F. orientalis* (Caucasus). The great majority of symbols are concentrated in the grasslands and deserts.

The VEGETATION MAP has one great advantage over the GEBOTANICAL MAP: the vegetation is shown for the entire land area on the map and is not limited to the Soviet Union as on the GEBOTANICAL MAP. This permits the reader to see the relations of the vegetation of the Soviet Union to the vegetation beyond the borders and to make enlightening comparisons.

A most important fact is that the legend of the GEBOTANICAL MAP has been translated into English (published in pamphlet form, 1956). This was most considerate of our Soviet colleagues and makes the maps useful to students of vegetation all over the world. Wherever a literal translation can leave any doubt in the mind of an English speaking reader, further elaboration of the point is given in brackets. These supplementary comments are indeed enlightening and it was a happy thought to include them in the legend. References to plants are usually made by generic and specific names. In 32 instances Latin versions of the vegetation types have been added for further clarification (e.g. *Querceta pubescentis*, *Lariceta fruticulosa et herboso-fruticulosa*, or *Prata substepposa*).

The two maps supplement each other and so permit the reader to obtain a deep insight into the geographical distribution of the vegetation of the Soviet Union. Quite incidentally, they reveal the enormous progress made by Soviet vegetationists during the past 20 years. The maps no longer show abstract schematic vegetation zones but portray real conditions in their latitudinal and altitudinal sequences, and within these broader features appear the longitudinal variations and local details. Those who have mastered the Russian language will wish to refer to the two-volume description of the vegetation of the U.S.S.R. which was published as an elaborating supplement to the maps. But the maps are quite independent of any text. They represent Soviet vegetation mapping at its best and are indispensable to all students of Soviet vegetation. Beyond that, the maps are valuable in vegetation studies of Eurasia as a continent, and are a major achievement in the field of vegetation mapping.

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¹ Lavrenko, E.M. & V. B. Sochava. 1956. Descriptio Vegetationis U.R.S.S. ad U.R.S.S. Tabulam Geobotanicam Annotationes. (Russian, with Russian and Latin titles.) Leningrad: Academiae Scientiarum U.R.S.S. 2 vols., 970 pp., figs., and colored maps.

This volume is third in a series of three books on the smut fungi. The first two, by the senior author, contained

¹ Fischer, George W. & Charles S. Holton, 1957. Biology and control of the smut fungi. New York: Ronald Press Co. x + 622 pp., 107 figs., 9 tables. \$10.00

an analysis of the literature and a systematic account of the fungi in the order *Ustilaginales*.

This volume is a synthesis of the world literature on the biology and control of the smut fungi based on a bibliography of more than 3600 titles and information from original research which has not yet been published.

Its approach is necessarily autecologic since plant diseases rarely lend themselves to the type of study represented by synecology. Since most work on smut fungi has been restricted, by force of economic pressure from the farm and laboratory, to the more important smuts of crop plants, hardly more than a dozen of the 1162 known and accepted species of smuts are considered in detail.

Except for a species on *Juniperus* and two on *Selaginella*, all known species are parasitic on members of the Angiospermae. More than half of these occur on the Gramineae and about one tenth on the Cyperaceae. Other families with more than 25 species of these parasites include the Compositae, Polygonaceae, Ranunculaceae, and Liliaceae.

Smuts may cause infection and sporulate in any part of the host plant; but their commoner manifestations are found in the inflorescence, where their spore masses may replace ovaries or anthers, or in leaves and in stems. The mycelium may be perennial in a perennial host. In dioecious plants, anther smuts may cause the production of anthers which appear to be functional in a flower normally producing only ovaries. The function here, of course, is the production and dissemination of smut spores by pollen-carrying insects rather than the production of pollen.

Smuts have become established over a long period of time in such crop plants as wheat, barley, oats, corn, and onions. Several beetles and molds have become adapted to the use of smuts as food sources although little work has been done on this type of community. It has been observed that certain bacteria produce antibiotics which are effective against smuts, and that certain smuts can produce antibiotic substances in culture. Large numbers of smut spores in the air of grain-producing areas cause allergies in sensitized people. There are some references in the literature to experiments in which smuts, when eaten in large quantities by livestock, cause illness and even death. However, other experiments of an erratic nature have been reported which tend to show that the tested smuts are toxic to neither animals nor man. In fact, it appears that in certain cases the smut spores are quite palatable to the experimental animal.

Most of the book is devoted to different methods of approach to the study of these fungi as they affect cereal crops. The reasons for these approaches and methods

are well outlined. Following descriptions of symptomatology and secondary effects on the host plant is a thorough description of the life history and parasitism of various types of smut fungi. Knowing what happens to the host plant after infection is only part of the story of smut biology and control. Some smut fungi can complete their life cycle in artificial culture, and all can be cultivated for at least part of their cycle in the laboratory. Techniques for handling such cultures and for learning the various facets of variation and sexuality are outlined carefully. Laboratory study is largely cytological, leading to intensive studies on the genetics of this group, their variability, hybridization, and mutation ability. For instance, *Ustilago maydis*, the common or boil smut of corn, produced over 220 mutants from a single line in a single year. Physiologic specialization is an important phase of this study; and in the development of new races of host plants resistant to smut infection, host variety reaction and the genetics of smut resistance are basic to an understanding of techniques and parental lines on which to base new resistant varieties.

Considerable space is given to the development of methods and techniques for the study of these organisms.

The authors note that it is only 200 years since stinking hunt of wheat was shown to be infectious, that only 100 years ago boil smut of corn was thought by learned men to be a physiologic disturbance due to excess cell sap, and that host-specialized races in the smut fungi have been known for only 35 years. The fact that extensive control methods using various types of chemicals designed to kill spores in the soil, or treatments designed to kill mycelium in the seed, are only partially effective, and the fact that smut fungi still cause millions of dollars of loss annually is a paradox which emphasizes "how feeble is the human effort when pitted against the forces of nature."

For the crop ecologist, the human ecologist, the anthropologist, the historian, the geneticist, the phytopathologist, and all the other "-ist's" whose trails may cross in this volume, "Biology and Control of Smut Fungi" is a well-presented and highly readable autecology of a very important order of fungi, the smuts.

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THE WATER RELATIONS OF TERRESTRIAL ARTHROPODS¹

To the millions of organisms inhabiting terrestrial and marine environments, the ability to retain water in the face of the inexorable loss thereof through excretion, evaporation and osmotic insults of the environment represents one realistic index of their success as inhabitants of their ecological niches. To biologists, especially ecologists and physiologists, interested in such problems of water loss and conservation, the many desirable features of small, easily-handled animals with high fecundity and availability in large numbers from inbred strains—*viz.*, insects—became obvious as early as 25 to 30 years ago. Indeed the preponderance of literature concerned with the water-environmental relationships of

arthropods, chiefly insects, will be found to occur during the period of 1930 to 1940 with the contributions of Buxton, Gunn, and Mellanby in England and of Chapman in this country, especially. Their application of quantitative methods and laws of physics to these problems of insect ecology marked a significant turning point in the methodology and rationale of such studies.

The fifth in a series of excellent monographs in experimental biology, this book represents a summary of more recent findings in this field in relation to the more numerous contributions of more than a decade ago, by one of the more recent contributors to the field of arthropod ecology. In treating the problem of water conservation by terrestrial arthropods the author has divided the book into four main sections, none of which can be truly separated from the others. These include the topics of water loss from transpiration in relation to cuticular structure, excretion and osmoregulation, water intake (in

¹ Edney, E. B. 1957. The water relations of terrestrial arthropods. Cambridge and New York: Cambridge University Press (Cambridge Monog. in Experimental Biol. 5). vi + 109 pp., 32 figs. \$3.00.

its various forms as free water, water vapor, and metabolic water), and the loss and conservation of water in relation to environmental temperature. As a well-written, well-edited book, this monograph suffers most from the author's having had to condense into 93 short pages of text and twelve pages of references the relevant data and literature of recent years as well as a fair part of the older literature normally covered in many more pages of the three major works in insect physiology (by Wigglesworth, Chauvin, and Roeder) as well as in textbooks of ecology. The author has nevertheless transected with obvious ease the several technical and theoretical lines of approach to this problem, in what is a particularly readable exposition and in a critical fashion. The summary chapter is especially helpful to the reader in such critical

appraisal of the data and their theoretical implications in its forceful presentation.

In serving a primary function of collating the data of recent years, for these several interrelated fields, and by placing them in their proper perspective in terms of older literature, this short treatment of a complex subject should prove especially useful to the non-specialist in entomology, the general ecologist and the general zoologist. To the beginning graduate student or researcher interested in such problems of arthropod ecology or physiology, it will prove especially helpful as an introduction to the general nature of the subject and as a summary of the literature.

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ANALYSIS OF RODENT POPULATIONS¹

This handbook serves as an outline for methods of accumulating and analyzing data concerning rodent populations. The techniques described will be familiar to the vertebrate ecologist, but in fact the booklet is intended for foresters, public health officers, and perhaps undergraduate college students, whose exposure to the methods and concepts of population ecology has been limited. However, the information is not easily accessible within the manual, for much is to be desired of its organization and no aid such as an index or full table of contents is offered; this is unfortunate in a manual intended to be simple and practical.

The information on making traps, setting out grids, recording of data from live-trapping and kill-trapping operations, population estimation, analysis of reproduction, mortality, and movements, covers the subject

excellently from the point of view of content, and comprises the first 68 pages. Pertinent literature is cited and appendix material concerns ectoparasites, collection and preservation of organs and tissues, and estimation of seed consumption by rodents. The standard, simple statistical aids in analyzing data seem particularly well-presented. Likewise, the caution necessary in interpreting analysis is appropriately emphasized. The illustrative material is clear and well-chosen, and the cover is an excellent example of good jacket design.

In addition to D. E. Davis, the contributors are V. F. Flyger, F. K. Hilton, J. J. Christian, R. Mansueti, R. Traub, R. Lord, and L. Adams. The booklet should well satisfy the need that inspired its publication, provided its reluctant internal organization can be hurdled.

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¹ Davis, David E. (editor). 1956. Manual for analysis of rodent populations. Ann Arbor: Edwards Bros. Lithoprinted, iii, + 82 pp., 10 figs., 13 tables. Available from David E. Davis, \$1.00.

A NEW SOCIETY AND BULLETIN OF SOIL ZOOLOGY

During the Sixth International Congress of Soil Science at Paris in 1956, zoologists specializing in the study of the fauna of the soil formed an international group with the object of providing a means for the exchange of information amongst workers in this field. To achieve this object a news bulletin is being published, and in addition international colloquia on particular aspects of the subject will be held at intervals.

The first number of the BULLETIN was published in May, and includes a questionnaire requesting details of current research projects together with information on animal groups studied. The results of this enquiry will be published in future numbers of the BULLETIN. Anyone interested in this field of research, and who has not received the BULLETIN, may obtain a copy by writing to: Mr. J. d'Aguilar, Station centrale de Zoologie agricole,

Route de St.-Cyr, Versailles, France.

The first colloquium devoted to "Methods of Research in Soil Zoology" will be held at Rothamsted Experimental Station, Harpenden, Herts., England, from the 10th to the 14th of July, 1958, immediately prior to the International Zoological Congress to be held in London. Paul W. Murphy, of the Rothamsted Experimental Station, is serving as the organizing secretary. The next number of the BULLETIN will give the programme and other details of the Colloquium.

HERMANN GISIN
(Vice-president of the Biology Commission
of the International Society
of Soil Science)

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NATURAL HISTORY MUSEUM

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